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PHYLOGENY AND ~~CLASSIFICATION~~ OF THE
CHAMAELEONIDAE (SAURIA) WITH SPECIAL
REFERENCE TO HEMIPENIS MORPHOLOGY

by

Charles Klaver and Wolfgang Böhme

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ABSTRACT

In the present study the hemipenis morphology of 28 *Chamaeleo* species and 2 *Brookesia* species is described. Data on hemipeneal morphology of 44 *Chamaeleo* species and 15 *Brookesia* species available from literature are reviewed. The combined data, comprising approximately 70 % of the known chameleon species, are analysed and discussed, i. e. the homology of hemipenis characters is demonstrated and their relative apo- or plesiomorphy established. Subsequently a phylogeny of chameleons based on hemipeneal characters is formulated. The hemipenis character transformation series are compared with similar series of karyological, osteological and lung-morphological character sets and the congruence of polarity demonstrated. The data of the different character sets are combined into a phylogeny of chameleons. This phylogeny is discussed in relation to zoogeographic hypotheses, especially that concerning the vicariance of Malagasy and African species. The current classification of chameleon species that are lumped together in two genera, viz. *Brookesia* Gray, 1864 and *Chamaeleo* Laurenti, 1768, does not coordinate with the phylogenetic relationships discussed. Therefore a revised classification is proposed: within the family Chamaeleonidae two subfamilies are recognized, viz. the Brookesiinae and the Chamaeleoninae. Furthermore, within the Brookesiinae two genera are recognized, viz. *Brookesia* and *Rhampholeon*, and within the Chamaeleoninae four genera are recognized, viz. *Calumma*, *Furcifer*, *Bradypodion* and *Chamaeleo*.

INTRODUCTION

The study of the structure of male external genitalia has proven to be very useful considering the consequences for the systematics and classification of many divergent groups. If we restrict ourselves to the Squamata it is especially in snake systematics that the study of the hemipenes has been incorporated as a routine in systematic practice (Cope 1894 & 1895; Dowling & Savage 1960). Hemipeneal studies in lizards are less common and, moreover, seldom leave the descriptive stage although there are, mostly recent, exceptions, e. g. Cope (1896), Böhme (1971), Arnold (1973, 1983) and Branch (1982). The Chamaeleonidae seem to be an exception as far as the number of papers on hemipenis morphology is concerned, the nature of these papers is, however, mostly fairly descriptive.

Cope (1896) introduced the study of hemipenis morphology to chameleon systematics when he mentioned some structural characteristics of the hemipenes of *Chamaeleo chamaeleon*, *C. gracilis*, and *C. pardalis*. Some 50 years later McCann (1949) and Loveridge (1953) described the hemipenes of *C. zeylanicus* and *Brookesia platycephs* respectively. Only in 1965, however, Domergue started a very successful period of study with regards to chameleon systematics in general and hemipeneal morphology in particular. Numerous new species of the genera *Brookesia* and *Chamaeleo* from

Madagascar were described by him and his colleagues. Moreover, the meagre knowledge of hemipeneal morphology was greatly expanded by the numerous detailed descriptions of the hemipeneal structure in these new but also already known species. Information on the hemipenes of the following taxa was recorded:

Brookesia bettschi (Brygoo, Blanc & Domergue 1974 b), *B. bonsi* (Ramanantsoa 1979), *B. ebenau* (Brygoo, Blanc & Domergue 1974 b and Brygoo & Domergue 1971), *B. legendrei* (Ramanantsoa 1979), *B. n. nasus* (Brygoo, Blanc & Domergue 1972 a), *B. peyrierasi* (Brygoo & Domergue 1969 d, 1975), *B. ramanantsoai* (Brygoo & Domergue 1975), *B. stumpffi* (Brygoo, Blanc & Domergue 1974 b), *B. therezieni* (Brygoo & Domergue 1970 a), *B. thieli* (Brygoo & Domergue 1969 b), *B. tuberculata* (Brygoo & Domergue 1975), *B. vadoni* (Brygoo & Domergue 1968), *Chamaeleo angeli* (Bourgat 1971), *C. balteatus* (Brygoo & Domergue 1969 c), *C. belalandaensis* (Brygoo & Domergue 1970 b), *C. bifidus* (Domergue 1965 and Ramanantsoa 1978), *C. boettgeri* (Brygoo 1971), *C. b. brevicornis* (Domergue 1965 and Brygoo & Domergue 1970 c), *C. b. hilleniusi* (Brygoo, Blanc & Domergue 1973), *C. b. tsarafidy* (Brygoo & Domergue 1970 c), *C. campani* (Domergue 1965), *C. capuroni* (Brygoo, Blanc & Domergue 1972 b), *C. cucullatus* (Brygoo & Domergue 1970 c), *C. g. gastrotaenia* (Domergue 1965 and Brygoo, Blanc & Domergue 1970), *C. g. andringitraensis* (Brygoo, Blanc & Domergue 1972 b), *C. g. guillaumeti* (Brygoo, Blanc & Domergue 1974 a), *C. g. maro-jezensis* (Brygoo, Blanc & Domergue 1970), *C. labordi* (Domergue 1965), *C. lateralis* (Domergue 1965), *C. malthe* (Brygoo & Domergue 1970 c), *C. minor* (Ramanantsoa 1978), *C. nasutus* (Domergue 1965), *C. oustaleti* (Domergue 1965 and Bourgat & Brygoo 1968), *C. pardalis* (Domergue 1965 and Bourgat 1969), *C. parsonii* (Domergue 1965 and Brygoo, Blanc & Domergue 1972 b), *C. petteri* (Brygoo & Domergue 1969 a and Ramanantsoa 1978), *C. peyrierasi* (Brygoo, Blanc & Domergue 1974 a), *C. rhinocerus* (Domergue 1965), *C. tigris* (Bourgat & Domergue 1971), *C. tuzetae* (Brygoo, Bourgat & Domergue 1972), *C. verrucosus* (Bourgat & Brygoo 1968) and *C. willsii* (Brygoo & Domergue 1966). In his two monographs on Malagasy chameleons Brygoo (1971, 1978) summarized the hemipeneal characteristics of most of these species.

Recent literature concerning the hemipeneal characteristics of African chameleons is far less comprehensive and ranges from incidental observations on the hemipenes of *Brookesia platyceps*, *B. marshalli*, *B. nchisiensis*, *Chamaeleo dilepis*, *C. melleri*, *C. mlanjensis* and *C. pumilus* (Broadley 1971), to detailed descriptions of the hemipenes of a particular species, viz. *C. chamaeleon* (Klaver 1981 a) and *C. calcaricarens* (Böhme 1985) or of the species of a particular species group, viz. *C. pumilus* cum suis (c. s.) (Raw 1976) and *C. bitaeniatus* c. s. (Böhme & Klaver 1980).

As a result of these studies our knowledge of the hemipenis morphology of Malagasy species is virtually complete, whereas that of African species is still fragmentary. Moreover, the descriptive terminology is both confusing and inconsistent because 1) different languages were used, 2) different authors using the same language coined different terms to similar structures and 3) in successive articles the same author(s) used the same term for different parts of the hemipenes.

In this paper we shall first introduce a more uniform terminology relating to hemipeneal characters as found in chameleons to remedy this terminological confusion. Subsequently, we shall employ this terminology to describe the hemipenes of a large number of mainly African chameleons. The combined descriptive data will then be compared, the observations and interpretations of previous authors commented on and the nature of the perceived similarities and differences in hemipeneal morphology evaluated and discussed. This is not to say, of course, that hemipenis characters have not been compared previously to confirm or refute assumed affinities (cf. literature cited above). However, the descriptive nature of most of these studies and the lacunae in the knowledge of hemipenis morphology in the Chamaeleonidae thus far forestalled the comparisons to lead to a formulation of hypotheses concerning the homology of various hemipenis characters, the sequence of character transformation and the phylogenetic relationship of chameleons at large. The hemipenis character transformation series are compared with similar series of other character sets, notably karyological, osteological and lungmorphological ones, to establish the amount of (in-) congruence between the various series. Only the knowledge of lung-morphological and hemipeneal characters is sufficiently complete to allow the construction of complete transformation series. Data concerning karyological and osteological characters are fragmentary, but sufficiently distributed among chameleon species to give an indication of polarity that can be compared with the ones of the complete series. A phylogeny of Chamaeleonidae based on hemipeneal characters is formulated and compared with the phylogeny as proposed by Klaver (1981 b) with the help of lung-morphological characters. It is demonstrated that like synapomorph lungcharacters synapomorph hemipenis characters are indicative of monophyletic groups at supra-specific level, thus defining clusters of related species. Lastly a phylogeny based on the combined data is constructed and discussed in relation to zoogeographic data. The phylogeny enables us to reconsider the present classification of the Chamaeleonidae in two genera, viz. *Brookesia* Gray, 1864 and *Chamaeleo* Laurenti, 1768. If the classification of chameleons is to coordinate with the phylogenetic relationships as deduced from the corporate comparative data then a revised classification has to be proposed. This revised classification presented in this paper is, of course, still provisional and to be tested with the help of additional comparative studies on other character sets. We think, however, it provides a proper framework for these studies to start from and, eventually, to improve on.

MATERIAL AND METHODS

The material of this study originates from the following institutions (followed by the institutional acronyms in parentheses):

British Museum (Natural History), London (BM),
Muséum d'Histoire Naturelle, Genève (MHNG),
National Museum, Bulawayo (RMB),
Naturhistorisches Museum, Vienna (NHMW),

Universitetets Zoologiske Museum, Copenhagen (UZM),
Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK),
Zoologisch Museum, Amsterdam (ZMS),
Zoologisches Museum der Universität, Berlin (ZMB),
Zoologisches Museum der Universität, Hamburg (ZMH), and
Zoologische Staatssammlung, München (ZSM).

The acronyms used are according to Duellman et al. (1978) and Leviton et al. (1980). Most of the material originates from the rich collection of the ZFMK, where it is a general policy to conserve as many specimen with everted hemipenes as possible. The method of hemipenes preparation is sufficiently known from literature (cf. Böhme 1971), in addition to everted hemipenes numerous inverted hemipenes were prepared and studied in the way described by Böhme & Klaver (1980). In case of these inverted hemipenes and of hemipenes strongly resembling the previously described one no illustration will accompany the description.

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STRUCTURAL TERMINOLOGY OF THE CHAMAELEONID HEMIPENES

Figure 1 and 2 provide schematic drawings of chamaeleonid hemipenes that unite the principal ornaments presently known in a combination that will, however, never be observed in nature. In the following lengthy but necessary review we revise the existing and confusing terminology pertaining to these ornaments and propose a limited number of general terms with which hemipenis characters can be described adequately. For instance, the term 'calyces', indicating the ornamentation of the mesial part of the hemipenes, originates from Cope (1896) and has generally been used in literature on snake and lizard hemipenes ever since. Not in the French literature however, that excels in proposing new terms. 'Cellules' (Domergue 1965), 'réseau de cellules polygonales'

(Brygoo & Domergue 1969 c), 'alvéoles polyédriques' and 'réseau alvéolaires' (Bourgat 1971) have been used instead to name only a few of the synonyms. Variation in hemipenis morphology must, of course, be acknowledged, but when characters do not seem to differ significantly new terms are superfluous. Therefore we shall treat as synonyms the different terms found in literature that indicate (sometimes quite) dif-

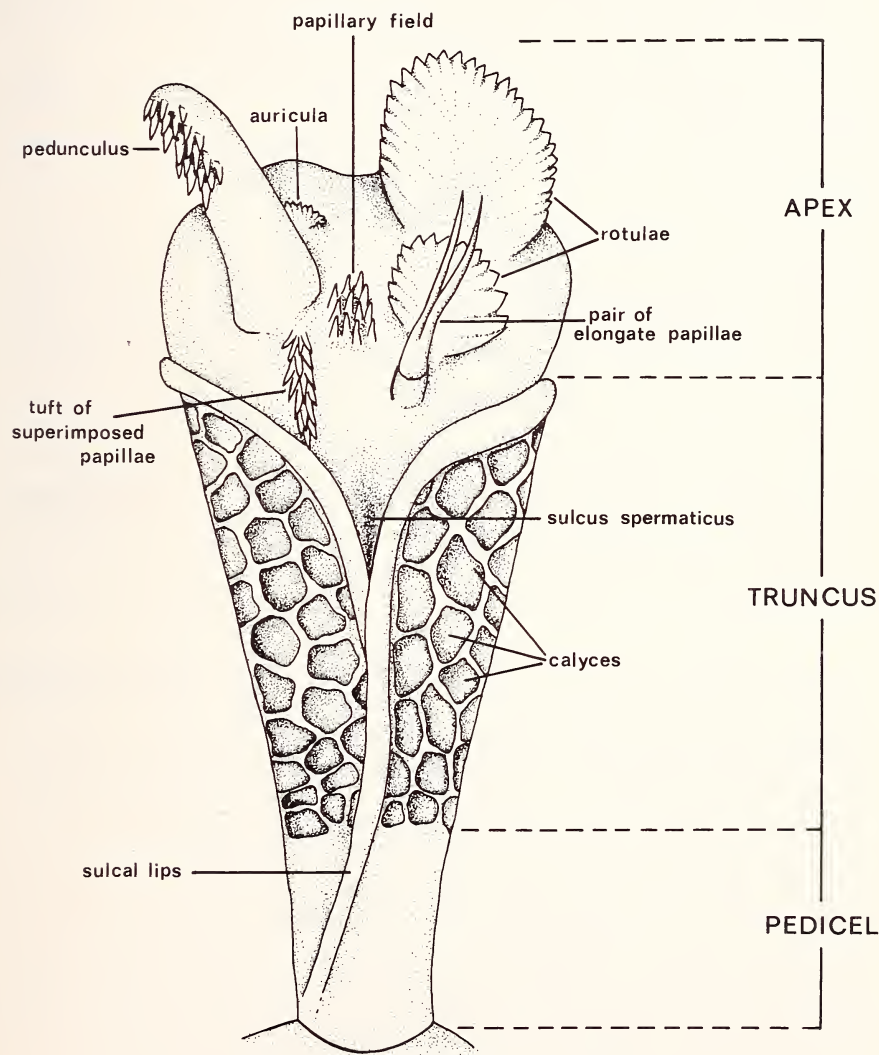


Fig. 1. Schematic hemipenis, uniting the principal characters found in the genus *Chamaeleo*. For explanation of terms see text.

ferent states of the same character. We are fully aware that this proceeding implies a less descriptive attitude and involves a good deal of interpretation. We think, however, this is justified by the remaining text of our paper. Besides, almost every paper can be considered a fraud the way it presents the sequence of data gathering, discussion and conclusions as the distinction between description and evaluation is not an absolute one. Major synonyms will be indicated between punctuation marks and when the same term has been used to indicate different parts of the hemipenis it will be commented on separately. Finally new terms will be introduced when a proper terminology is not available and, of course, when entirely new structures are described.

In the ordinary chameleons (genus *Chamaeleo*, Fig. 1) the shape of the everted hemipenis is generally subcylindrical or slightly clavate. In the pygmy chameleons (genus *Brookesia*, Fig. 2) the everted hemipenis is mostly strongly clavate. In both groups the hemipenes are simple or at the most slightly bilobed at the distal end. In a hemipenis the following parts can be distinguished:

Proximal part or pedicel (derived from pediculus = diminutive of pes = foot) i. e. a relatively short basal part of the hemipenis that is characterized by its smooth surface (synonyms: 'pedicil', McCann 1949 partim; Böhme & Klaver 1980 and Klaver 1981 a; 'pédoncule', Brygoo & Domergue 1969 c and subsequent French papers on the subject).

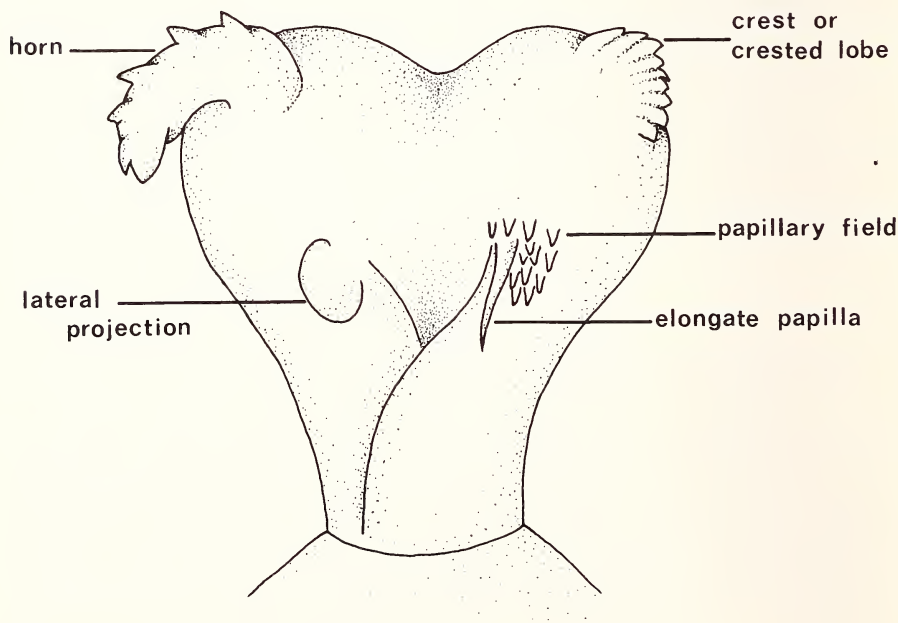


Fig. 2. Schematic hemipenis, uniting the principal characters found in the genus *Brookesia*. For explanation of terms see text.

Mesial part or truncus (synonyms: 'pedicil', McCann 1949 partim and 'corps', Bourgat & Domergue 1971 a. o.) In *Chamaeleo* the truncus is ornamented with shallow pockets between retiform ridges that are commonly known as calyces, hence the surface is said to be calyculate (synonyms: 'reticulately honeycomb-like pits', McCann 1949 and the terms mentioned at the beginning of this section). The calyces may vary in depth, size and shape, the ridges surrounding them may either be smooth, fringed, serrated or denticulated at the outer margin. In several species the calyces are so deep that the surrounding ridges overlap and give the truncus a laminate appearance. Other terms relating to this condition are: 'flounced', 'ridged' and 'plicated' (Cope 1896 and McCann 1949); 'franges cellulaires' and 'collerettes superposées à bord frangé' (Brygoo & Domergue 1969 c). If the free margin of the ridges is extremely fringed the entire truncus appears to be coarsely papillate. In *Brookesia* the truncus bears no calyces and has a smooth surface, consequently a distinction between pedicel and truncus is not possible.

Longitudinally along the pedicel and the truncus runs the sulcus spermaticus bordered by sulcal lips (synonyms: 'gouttière', Bourgat & Brygoo 1968 and 'sillon', Brygoo & Domergue 1969 c). As to the sulcal lips the following synonyms have been recorded: 'lèvres du sillon', Bourgat 1971 and 'lèvres externe' and 'interne', Bourgat & Brygoo 1968 a. o. The surface of the sulcus is always smooth, that of the lips may either be smooth or set with traces of the ridges that surround the calyces. The sulcal lips may diverge distad and continue as a ridge that encircles the distal part of the hemipenis, thus clearly separating this latter part from the truncus. If this ridge is present the condition is called capitate. The ridge itself is known under the name 'collerette' (Bourgat & Brygoo 1968) and 'bourrelet' (Bourgat 1969). In the non-capitate condition the distal part of the hemipenis and the truncus can also be differentiated, because the truncus bears calyces whereas the distal part does not (for terminology relating to this condition see below). In *Brookesia* no such distinction can be made because of the absence of calyces as well as the capitate condition.

Distal part or apex. The apex may be single or slightly bilobed and bears mostly an elaborate ornamentation. The various ornaments are generally arranged in bilateral symmetry, i. e. ornaments are present in pairs, making the left part of the apex a mirror image of the right part (unlike Figs. 1 and 2, in which for the sake of brevity the principal, mostly paired ornaments are depicted singly). The plane of symmetry is thought to run lengthwise through the hemipenis from the upper or truncal part of the sulcus spermaticus to the opposite asulcal surface of the hemipenis. Single ornaments are generally situated medially at the apex in the plane of symmetry. All apical ornaments are mostly confined to the sulcal-central surface of the apex, although this condition may be exaggerated by insufficient eversion of the hemipenis. The apical surface surrounding the ornaments is smooth (synonyms indicating this condition: 'membranous apron', Cope 1896; 'partie terminal lisse', Bourgat & Brygoo 1968; 'dôme', Bourgat 1969 and 'dôme lisse', Ramanantsoa 1978). In *C. chamaeleon* and *C. zeylanicus* the apex bears a papillate or serrate transverse ridge ('glottis-like structure', McCann 1949 and 'Reihe von Papillen', Klaver 1981 a). The ornamentation of the apex may include the following components:

a) Papillae, i. e. fleshy and pliable projections varying in size and shape from short to elongate, from blunt to pointed and from broad to slender, can be found on the hemipenes of both *Brookesia* and *Chamaeleo* species. Papillae may either be single, grouped in pairs or rows, evenly scattered over the apex or concentrated on various locations on the apex in papillary fields (Böhme & Klaver 1980). Especially near the median of the apex in either asulcal, central or sulcal position numerous small papillae-like structures or sometimes somewhat more complex structures have been described with the help of almost equally numerous terms. In *C. pardalis* a pair of small conical papillae (or one forked one) is present on either side of the median of the apex (Bourgat 1969). Similar but simple structures in *C. tigris* are called 'ergots' (Bourgat & Domergue 1971). Still others are: 'mamelon médiane', 'protubérance polaire' and 'mamelon central' (Brygoo & Domergue 1970 c); 'relief median posterieur', 'protubérance mediane antérieure dedoublée' or 'simple' and 'mamelon antérieur médian' (Brygoo et al. 1970); 'barbule médiane' (Brygoo & Domergue 1969 a); 'relief médio-ventral' and 'mamelon médio-dorsale bifide' (Brygoo et al. 1972 b); 'cone' and 'languette (auricule) medio-sommitale denticulée' (Ramanantsoa 1978). Despite the morphological variation we like to indicate these structures, if appropriate, with the general term 'papillae', eventually specified with additional descriptive terms, instead of describing them with the help of a multiplicity of terms. We acknowledge, of course, recurrent distinctive papillate structures on the hemipenes of various species. For instance, Brygoo & Domergue (1970 c) described two groups of papillae that are present on the hemipenes of *C. brevicornis*, each group consisting of two elongate papillae. Subsequently this character was also found in *C. cucullatus*, *C. gastrotaenia andringitraensis*, *C. g. guillaumeti*, *C. malthe*, *C. peyrierasi* and *C. tigris* (Brygoo et al. 1970, 1972 b, 1973, 1974 a and Bourgat & Domergue 1971; 'barbillons bifides' and 'cornes bifides'). Another example are the tufts of superimposed papillae found in the hemipenes of *C. pardalis* and subsequently in those of other Malagasy species as well, e. g. *C. angeli* and *C. belalandaensis* (Bourgat 1969; Brygoo & Domergue 1970 b and Bourgat 1971; synonyms: 'barbillons' and 'languette plumeuses'). We could coin the two papillate structures mentioned with terms like furculae and barbulae respectively to indicate their singularity and, simultaneously, improve the terminology. How appropriate this may seem though, it is neither necessary nor particularly helpful, because the structures are clearly papillate and can conveniently be described as such (see above). Moreover, it is far more important to recognize a pattern in the variation of morphological characters than to name each character separately. As a matter of fact terminological constraint would very much have facilitated this recognition of pattern as we were to find out ourselves while preparing this paper. Moreover, the terminology may be premature as further study may reveal the structures under consideration to be but one out of a set of homologous characters that may either be simpler or more complex, thus rendering the proposed terms too wide or too narrow to be useful. Therefore we shall restrict ourselves in the use of terms that relate to papillae or papillate structures.

b) Pedunculi (singular: pedunculus = stalk, cf. Fig 1). One pair of pedunculi may be present at the sulcal side of the apex. Pedunculi are in their basic form thick stalks in-

deed, that protrude over the distal end of the sulcus spermaticus. The sulcal surface of the pedunculi is mostly set with numerous pointed papillae that are often arranged in rows. This general form may be modified in the various species. The pedunculi may be less elongate and curved towards the asulcal side of the apex, thus projecting their papillae upwards (*C. pardalis*, Bourgat 1969). In other species the pedunculi may take the form of papillate or crested lobes (*C. angeli*, Bourgat 1971 and *C. tuzetae*, Brygoo et al. 1972) or twist lengthwise to form a cusp at their distal end (*C. petteri*, Ramanantsoa 1978). Despite this variation (that will be partially explained at the end of this section) all are considered to represent the same character and are, consequently, to be coined with the term pedunculus.

It must be noted that in this paper we revert to the latinized version of the word 'pédoncule' sensu Bourgat & Brygoo (1968) and its original meaning, i. e. indicating a stalk-like apical ornament. In subsequent French literature, starting with Brygoo & Domergue (1969 c), the term 'pédoncule' is suddenly and without argumentation attached to the basal part of the hemipenes, in this paper indicated with the term pedicel. To complicate the matter even further Ramanantsoa (1978) used 'pédoncule' again to indicate both a papillate apical lobe and the basal part of what is here considered a pedunculus. Such a differentiation between the basal and the distal part of pedunculi occurred frequently, but in most cases the term 'pédoncule' was not employed, e. g. 'lobe, bourrelet' and 'épines souples' together (Brygoo & Domergue 1970 b) correspond with a pedunculus. In Ramanantsoa (1978) 'pédoncule, lobe and cornes latéro-supérieure' correspond with a pedunculus. A possible explanation as to why the basal part of either the hemipenis itself or the pedunculi are indicated with the term 'pédoncule' might be a confusion of this term with the diminutive of the term pes, i. e. pediculus.

c) Auriculae (singular: auricula = diminutive of auris = ear, cf. Fig. 1) The term 'auricule' was used for the first time in this context by Bourgat & Brygoo (1968) to indicate two curved denticulate ridges positioned opposite to the pedunculi at the asulcal side of the apex of the hemipenes of *C. oustaleti* and *C. verrucosus*. In subsequent papers in which pedunculi-bearing hemipenes were described auriculae were mentioned to be present as well. Their shape may vary, however, in different species, e. g. the denticulate ridge may be divided in two parts (*C. verrucosus*) or instead of one, two neighbouring but distinct auriculae may be present, thus doubling the total number of auriculae to four (*C. bifidus* and *C. minor*, Ramanantsoa 1978). In still other Malagasy species the hemipenes were found to lack both pedunculi and auriculae and to bear two pairs of other apical ornaments instead, most of which were, however, also indicated with the term 'auriculae' (Brygoo & Domergue 1970 c; Bourgat & Domergue 1971 and Brygoo et al. 1970, 1972 b, 1973, 1974 a). However, these ornaments are, as compared with auriculae as found in pedunculi-bearing hemipenes, much more developed and shaped like semicircular plates or discs. The only resemblance to auriculae is their denticulate outer margin. Therefore we think (and we hope to elucidate this in the remaining text) the ornaments are not auriculae, but belong to a category of apical ornaments that will be discussed in the next paragraph. Consequently the denticulate ridges at the

asulcal side of the pedunculi are the only structures to be indicated with the term 'auriculæ', which is adopted here in its latinized form.

d) Rotulae (singular: rotula = diminutive of rota = wheel, cf. Fig. 1). This term is introduced here to indicate an apical ornament, originally found on the hemipenes of African species, for which no proper term is available. In general rotulae look like semicircular discs with a denticulated or serrated outer margin. The profile of the cross section is somewhat biconvex. On the surface shallow ridges may be seen to diverge from the base of the rotula to the outer margin, thus reminding of a *Pecten jacobaeus* shell (see Fig. 1). Various terms have been employed to describe them, viz. 'papillae', Cope (1896 partim); 'erect crescentic plates', McCann (1949); 'apical discs', 'wings' and 'cogwheels', Broadley (1971), Böhme & Klaver (1980) and Klaver (1981 b); 'inward curving denticulate apical structures', Raw (1976) and 'halbkreisförmige Strukturen', Klaver (1981 a). To avoid further terminological confusion we propose to designate these ornaments as rotulae, despite of the fact that in some species they are not so much rotund but more or less sickle-shaped. Two pairs of rotulae are generally present, viz. an asulcal and a sulcal pair (Böhme & Klaver 1980). In the species of the *C. chamaeleon*-group, however, up to five pairs may be found, i. e. in the sulcal position instead of one pair, two groups each composed of four rotulae may be present. The size of these sulcal rotulae may differ markedly, the largest of them being smaller than the asulcal rotulae (Klaver 1981 a). As we indicated above we think that the apical ornaments found in numerous Malagasy species and described as 'auricule' are in fact rotulae. We came to this conclusion not only by studying the descriptions available in literature, but also by examining the hemipenes of several of the species concerned, e. g. *C. brevicornis*, ZFMK 36320. Accepting this point of view results in the following amendment of the list of synonyms: 'disques apicaux', 'auricule semicirculaire', 'lame dentelée' or 'denticulée', 'lame pectinée', 'lobe antérieures', 'lame falciforme' and 'auricule', the latter term combined with one of the numerous epithets such as 'subapicales', 'dorso-laterales', 'medio-ventrales', etc. (Brygoo & Domergue 1970 c, Bourgat & Domergue 1971 and Brygoo et al. 1970, 1972 b, 1973, 1974 a). These very terms illustrate our point of view as some of them describe rotulae quite well.

The position and orientation of rotulae on the apex may vary considerably, especially in Malagasy species as can be inferred from the profuse terminology. Some caution as to these characteristics of rotulae and probably most other apical ornaments as well is necessary as they can easily be affected in the process of preparing the hemipenes for preservation in everted condition. Therefore we refrain from including epithets as the ones cited above in the terminology and employ rotulae as the only term to indicate the structure under consideration. The same applies to the terminology of other apical ornaments. This is not to say of course that in describing the hemipenes and their ornaments we shall refrain from using additional descriptive terms relating to position and orientation in clearcut cases or that we shall ignore conspicuous differences in ornament morphology.

Another factor that probably affects the structural characteristics of apical ornaments is the seasonal variation. The apical ornamentation of the hemipenes of *C. tuzetae*

(Brygoo et al. 1973), for instance, appears not fully differentiated, which corresponds with the date of capture (May) and the austral climatological conditions of the locality at the time of capture (S.W. Madagascar, rainy season: October till April). This observation is supported by the observations of Bourgat (1969) and Bouix & Bourgat (1970). They established a reproductive cycle in *C. pardalis* from Réunion and Madagascar and recorded a correlation between the timing of spermatogenesis, courtship-behaviour and egg-deposition, and the variation in climate. Under the local austral conditions this means that spermatogenesis lasts from December till June, with a two months interruption in the austral winter (December till April) and egg-deposition takes place at the end of the rainy season (March). Like Bourgat & Brygoo (1968) before him Bourgat (1969) found the number of papillae on the pedunculi to vary, but he did not relate this variation to the reproductive cycle. Brygoo & Domergue (1971) comment on the variation in hemipenis morphology in *B. ebenau* and propose as a possible explanation a seasonal variation in relation to the sexual activity. The specimen with less differentiated hemipenis ornamentation was indeed captured at the beginning of the dry season (May). Seasonal and hormonally controlled differentiation of hemipenis ornamentation has been established in Lacertidae by Böhme (1971). A thorough and documented study on this subject in the Chamaeleonidae will shortly be presented by Böhme (MS).

The apical ornamentation of *Brookesia* hemipenes is much more difficult to characterize with the help of the descriptions available in literature than that of *Chamaeleo* hemipenes. Several descriptions are useless because the hemipenes are, probably due to seasonal variation, devoid of any differentiated apical ornamentation whatsoever, e. g. *B. ramanantsoai*, *B. therezieni* and *B. tuberculata* (Brygoo & Domergue 1970 a, 1975). From the remaining descriptions one can infer that ornaments like pedunculi, auriculae and rotulae are absent in *Brookesia*. Instead of two pairs, as in *Chamaeleo*, only one pair of major ornaments is present (Fig. 2, see also Brygoo et al. 1972 a). This assertion should be considered tentative we hasten to add, because the development of other ornaments seems to suggest otherwise. In some species there is a prominent lateral projection, sometimes almost as large as what we consider here the major apical ornaments, that gives the hemipenes a trilobed, asymmetrical appearance, e. g. *B. griveaudi* (Brygoo & Domergue 1971, 1974 b). However, we believe this particular projection to be identical to less extremely developed lateral structures found in other species with an 'ordinary' dual apical ornamentation. This means that we consider the 'lobe externe' of *B. griveaudi* to be homologous with, for instance, the 'protubérance conique' of *B. stumpffi* (Brygoo et al. 1974 b). The observed differences may be genuine, eventually influenced both by the poor state of preparation of the hemipenes, as is often the case in *Brookesia*, and seasonal variation, or they may be apparent for merely the result of the two factors mentioned. The hemipenes of another specimen of *B. griveaudi* described by Brygoo & Domergue (1971) suggest this latter possibility.

Two types of dual apical ornamentation seem to exist in *Brookesia*, viz. horns and crests (Fig. 2). Horns are broad rotund projections, tapering towards the distal end and curving towards the sulcal side of the hemipenes. The asulcal surface is mostly set with

papillae. Synonyms are: 'recurved claw- or horn-like organs' set with a 'series of papillae', Loveridge (1953); 'curved apical horns', Broadley (1971) and 'apical spines', Klaver (1979). These ornaments have been described for African species only. The apical ornamentation of Malagasy species consists of two papillate or denticulate crests or crested lobes, somewhat unequal in size. This pattern is most clear in *B. betschi* and *B. nasus* (Brygoo et al. 1972 a and 1974 b) and although the pattern is less clear and/or more difficult to establish in other species we assume it to be the same (resulting in the following synonyms: 'auricule sommitale interne/externe', Ramanantsoa 1979; 'lobe antérieur/postérieur', Brygoo et al. 1974 b; 'auricule avec deux crêtes', Brygoo & Domergue 1971; 'deux hémisphères apicaux portent groupes d'ergots', Brygoo & Domergue 1969 d; 'lobe latéral/médial', Brygoo et al. 1972 a; 'lobe interne/terminal', Brygoo et al. 1974 b; 'apex interne/externe', Brygoo & Domergue 1969 b and 'lobe interne/externe', Brygoo & Domergue 1968). In some species there may be an additional ornamentation, e. g. lateral projections (see above), papillary fields (Brygoo & Domergue 1971) or elongate papillae ('languette', Brygoo & Domergue 1969 b and 'languette apicale', Brygoo & Domergue 1971). The above conception of hemipenes ornamentation in *Brookesia* may be too simplified and somewhat rash. However, well established is the dual aspect of the apical ornamentation and the fact that African and Malagasy species differ much more and more clearly so from one another in apical ornamentation than do either African or Malagasy species among themselves. As to the variation in apical ornamentation within the geographic subgroups of *Brookesia*, particularly the Malagasy species, our conclusion may indeed be rash and in need of additional studies on better material. The former two observations are, however, more significant for the present study than the supposed unity in apical ornamentation in Malagasy species.

DESCRIPTION OF THE HEMIPENES

Chamaeleo africanus Laurenti, 1768 (Fig. 3 a and b)

ZFMK 8828 Mora, N.Cameroon and ZFMK 38402 Erkowit, E.Sudan

Hemipenes subcylindrical with a relatively large pedicel, approximately one third to half of the total hemipenislength. The truncus is set with large and deep calyces, whose margins are extremely fringed, thus giving the truncus a papillate appearance. Sulcus spermaticus bordered by well developed sulcal lips that bear papillate ridges as well. The apex is crowned with numerous symmetrically arranged rotulae, viz. one asulcal pair and three sulcal pairs. The asulcal rotulae are smaller than the largest of the sulcal ones. The sulcal rotulae form two groups, each group consisting of three parallel and obliquely oriented rotulae, the median one the largest, the lateral one the smallest. All rotulae have denticulated margins. Laterally of the two groups of sulcal rotulae are two fringed flanges.

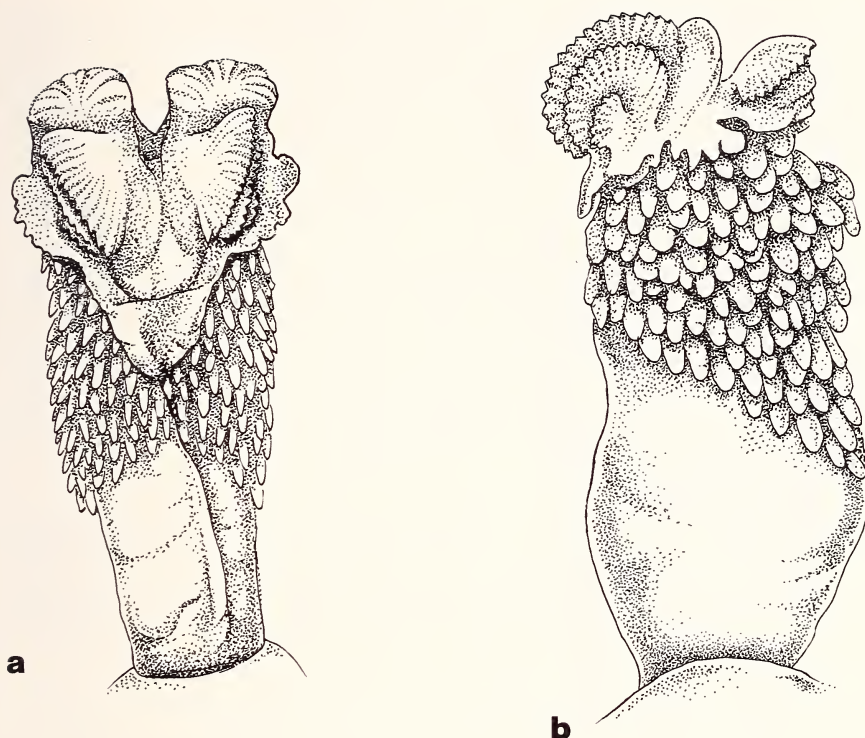


Fig. 3 a & b. Hemipenis of *C. africanus*. a = sulcal view, b = lateral view.

***Chamaeleo calyptratus* Duméril, 1851 (Fig. 4)**

ZFMK 29067 Sana, Yemen

Hemipenes clavate, pedicel one third of hemipenislength. Sulcal lips well developed and partially set with rows of minute papillae. The truncus is calyculate, i. e. proximally there are parallel ridges that interconnect gradually to enclose large transversely elongated calyces halfway the pedicel and the apex. The apex terminates in a pair of large sickle-shaped rotulae. Proximally at the sulcal side of these rotulae a partially serrated ridge can be seen to border an area in which two groups of smaller rotulae are positioned. Each group consists of two collateral rotulae of almost equal size that are oriented obliquely. All rotulae have a finely serrated margin.

***Chamaeleo calyptratus calcarifer* Peters, 1854**

ZFMK 41091 5 km north of the Yemen border, Saudia Arabia

Hemipenes as those of *C. calyptratus* with six rotulae on top of the apex.

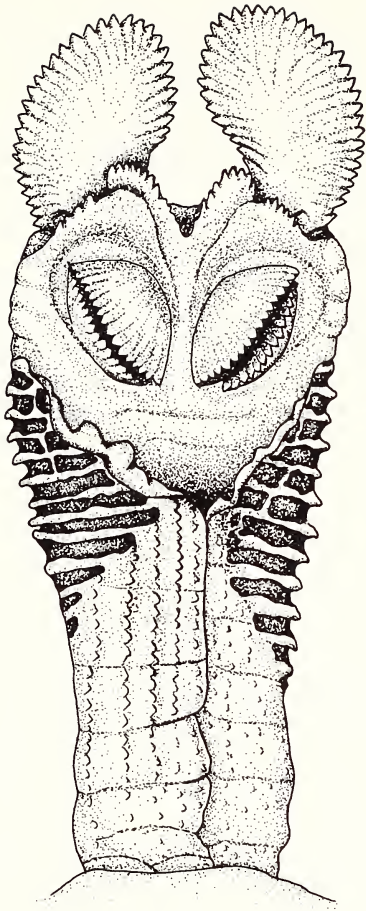


Fig. 4. Hemipenis of *C. calytratus*, sulcal view.

***Chamaeleo chamaeleon orientalis* Parker, 1938**

BM 1963-805 Rada, Yemen

The hemipenes of this subspecies fit the description of the hemipenes of the nominal form (Klaver 1981 a) except for 1) the more prominent development of the smallest rotulae of the sulcal rotulae groups and 2) the more sickle-shaped form of the asulcal rotulae.

***Chamaeleo arabicus* Matschie, 1893**

ZMB 11135 (holotype) Lahej near Aden, South Yemen; NHMW 7466:1 same locality

Hemipenis with only four elongate rotulae with finely denticulated margins. Calyces deep with serrated margins. This hemipenis ornamentation differs clearly from the one of *C. chamaeleon* (cf. Klaver 1981 a) of which *C. arabicus* was considered a subspecific

form (Hillenius 1963). Arnold (1980) noted that *C. c. arabicus* is as distinct from the nearest known *C. c. orientalis* specimens as some full species, such as *C. africanus*, are. He, therefore, treated *C. arabicus* as a megasubspecies (or semispecies?) of *C. chamaeleon*. Our present observations on the hemipenes justifies, we think, this form to be elevated to the specific rank.

***Chamaeleo zeylanicus* Laurenti, 1768**

ZFMK 39043, locality unknown

Hemipenes stout, pedicel one third of hemipenislength. Truncus set with calyces. Apical ornamentation consists of one pair of large somewhat elongate asulcal rotulae and three pairs of smaller sulcal rotulae, that are arranged in two groups. All rotulae have a serrate margin. The transverse ridge separating the asulcal rotulae from the sulcal ones is smooth. Differences with the original description of McCann (1949) are 1) the presence of three pairs of small sulcal rotulae instead of one pair and 2) the absence of a serration on the transverse ridge.

***Chamaeleo dilepis* Leach, 1819 (Fig. 5 a & b)**

ZFMK 18895 proximity of Mombasa, Kenya

Hemipenes clavate, pedicel approximately half of hemipenislength. The truncus is set with large and shallow calyces, whose bordering margins are coarsely denticulated.

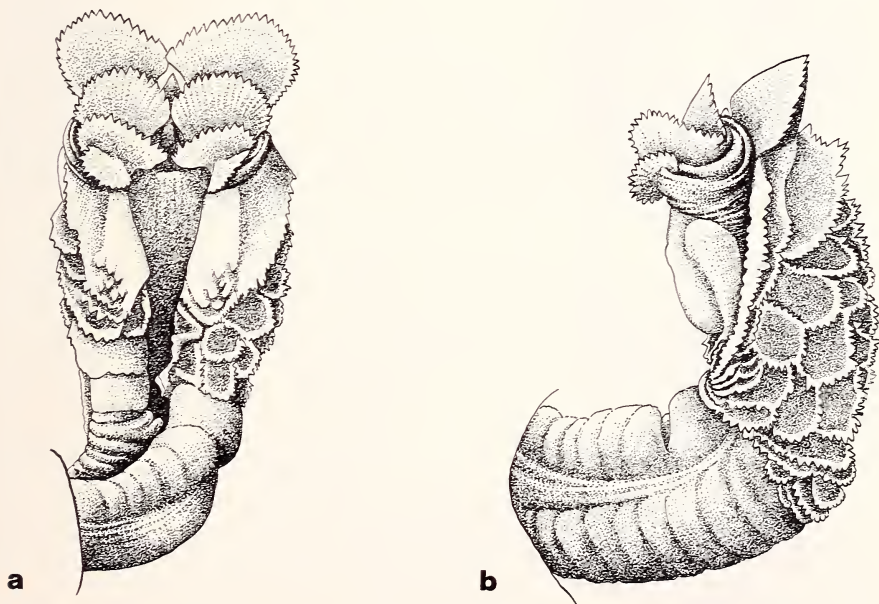


Fig. 5 a & b. Hemipenis of *C. dilepis*. a = sulcal view, b = lateral view.

Sulcal lips also partially calyculate. The apical ornamentation is very much like the one in the preceding species, viz. with one pair of asulcal rotulae and three pairs of sulcal rotulae. A difference is the transverse orientation of these latter rotulae. These observations correspond with those of Broadley (1971).

***Chamaeleo quilensis* Bocage, 1866**

RMB 24130 and 25487 Chisambo, Mlanje, Malawi and RMB 29495 Vumba Mts., Zimbabwe

The hemipenes of this form differ from those of the preceding form in some respects: 1) the calyces are small and deep and enclosed by irregularly fringed ridges, 2) the rotulae of the two sulcal rotulae groups are much smaller and are, moreover, 3) placed in a much more clearly defined apical area and 4) the median-distal border of this area bears several papillae, whereas there is only one large papilla in *C. dilepis*.

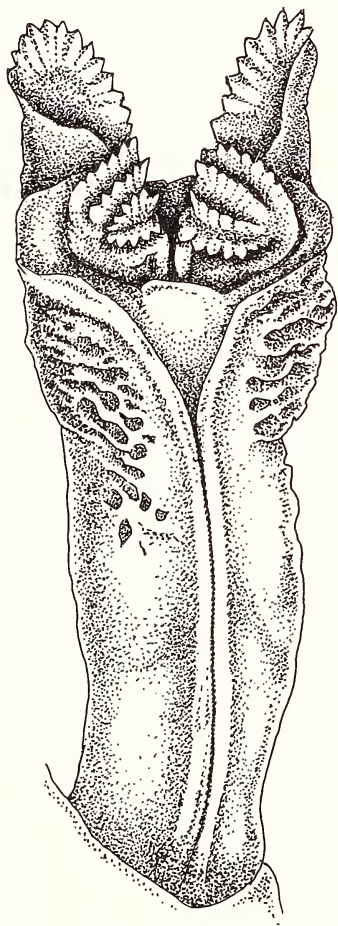


Fig. 6. Hemipenis of *C. senegalensis*, sulcal view.

***Chamaeleo gracilis* Hallowell, 1842**

ZFMK 8841 proximity of Kribi, S.Cameroon

Hemipenes subcylindrical, pedicel one third to half of hemipenislength. The truncus is set with calyces, enclosed by fringed margins, that extend mainly in transverse direction. Apical ornamentation with four pairs of rotulae, all transversely oriented. One large conical papilla between the asulcal rotulae. Sulcal lips without ornamentation.

***Chamaeleo senegalensis* Daudin, 1802 (Fig. 6)**

ZFMK 17312 Bandia, Senegal and ZFMK 27399 N.Togo

Hemipenes subcylindrical, pedicel one third to half of hemipenislength. Sulcus spermaticus bordered by well developed and unornamented sulcal lips. Small calyces confined to the distal part of the truncus, especially the medial surface; more proximal calyces are larger and elongate. The apex is crowned with two large rotulae, each positioned on top of a basal projection. Proximally at the sulcal side of these projections are two groups of smaller rotulae, each group composed of four collateral rotulae. The inclination of these rotulae with the hemipenis length-axis is exactly the opposite of the one found in, for instance, *C. calypttratus*. The large asulcal rotulae have a different orientation as well, viz. instead of being oriented in the same transverse plane (cf. *C. calypttratus*) they lie in almost parallel planes. All rotulae have a coarse denticulation of hooklike denticles, that may, however, be due to seasonal variation.

***Chamaeleo laevigatus* Gray, 1863**

ZFMK 29738 Talanga forest, South Sudan

Hemipenes not unlike those of *C. senegalensis*, except for the rotulae arrangement. Instead of ten, eight rotulae are present on the apex, two large asulcal ones and six sulcal ones, the latter arranged in two groups of three collateral rotulae. Margins of the rotulae coarsely serrated. On account of this profound difference in rotulae number *C. laevigatus* is treated here as a full species and not as a subspecies of *C. senegalensis*.

***Chamaeleo namaquensis* Smith, 1831**

ZFMK 7983 Gobabeb, S.W.Africa and ZMA 15195 Namib Desert Park, S.W.Africa

Hemipenes with only two pairs of rotulae, viz. an asulcal pair and a sulcal pair. All rotulae are more or less semicircular, denticulated and have approximately the same size. Calyces enclosed by fringed ridges.

***Chamaeleo oweni* Gray, 1831 (Fig. 7)**

MHNG 1012-1 Foullassi, Cameroon

Hemipenes stout and truncated, pedicel one third of hemipenislength. The truncus is covered with large and deep calyces. The ridges that surround the calyces extend medially over the apex of the hemipenis towards the sulcal side, where they gradually dissolve in fleshy fringes and papillae. The apex bears four sickle-shaped rotulae of equal size, grouped in an asulcal pair and a sulcal pair. The margins of the rotulae are finely ser-

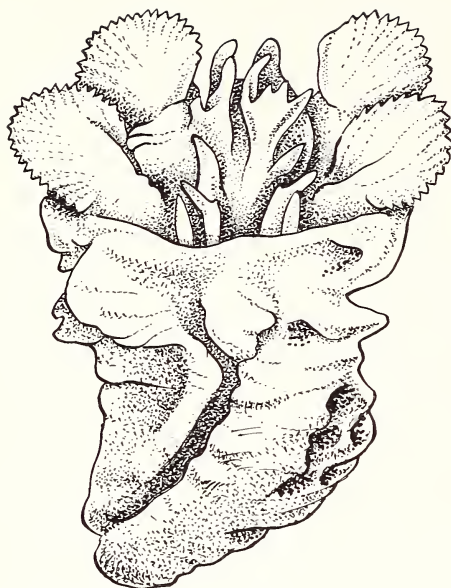


Fig. 7. Hemipenis of *C. oweni*, sulcal view.

rated. At the base of each sulcal rotula is a large fleshy papilla; medially and somewhat distally of these papillae another pair of isolated papillae is present.

***Chamaeleo montium* Buchholz, 1874 (Fig. 8)**

ZFMK 8844, 9067, 9069, 15287 and 15288 Buéa, Mt. Cameroon, Cameroon

Hemipenes stoutly built and truncated, pedicel one third of hemipenislength. The truncus is coarsely calyculate, the well developed sulcal lips and sulcus spermaticus without ornamentation. Apex with two pairs of small denticulated rotulae. The rotulae are positioned towards the sulcal side of the hemipenis, so they cannot be observed from the asulcal side (cf. the hemipenis of *C. hoehnelii*, Böhme & Klaver 1980). Numerous fleshy papillae are concentrated in two symmetrically arranged fields medially of the sulcal rotulae. Up to 16 papillae/field may be present.

***Chamaeleo cristatus* Stutchbury, 1837**

ZMA 10157 Foulassi, Cameroon

The hemipenes of this species resemble those of *C. oweni*. The apex possesses also four sickle-shaped rotulae with minutely serrated margins. The ridges of the calyces extend over the apex and dissolve gradually in fringes and finally in papillae. A major difference is the presence of numerous papillae grouped in two symmetrically arranged papillary fields that are located next to the sulcal rotulae. Each field consists of 8 to 9 papillae. Moreover, a few scattered papillae are present between these papillary fields.

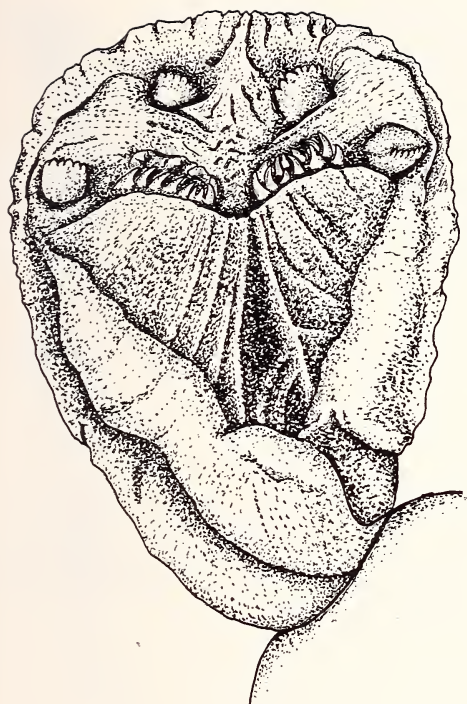


Fig. 8. Hemipenis of *C. montium*, sulcal view.

***Chamaeleo johnstoni* Boulenger, 1901**

ZMA 11959 Goma, Zaire

The hemipenes have two pairs of small semicircular rotulae with denticulated margins. The ridges of the calyces continue over the apex and dissolve gradually in fringes and papillae. The last of these papillae are positioned between the sulcal rotulae. Near the base of these rotulae are a few scattered papillae and a little more medially and proximally are two papillary fields with 4 to 5 papillae each. Except for the rotulae the hemipenes are set with diffusely dispersed melanophores.

***Chamaeleo quadricornis* Tornier, 1899**

ZFMK 15291 and 15292 Mt. Lefo, N.Cameroon

Hemipenes not unlike those of *C. montium*. Calyces smaller and shallower. Two pairs of small denticulated rotulae are present, as well as two papillary fields with up to 9 papillae/field, that are, however, situated a little more proximally of the sulcal rotulae than in *C. montium*.

***Chamaeleo camerunensis* Müller, 1909**

ZSM 484-1909 Bibundi, Cameroon

Hemipenes as in the preceding species, i. e. with two pairs of denticulated rotulae and near the base of each sulcal rotula a papillary field with up to 10 fleshy papillae.

***Chamaeleo feae* Boulenger, 1906**

ZFMK 9381 Moca, Fernando Po

Also in this species two pairs of denticulated rotulae and at the base of each sulcal rotula a large papillary field with up to 16 elongate papillae.

***Chamaeleo eisentrauti* Mertens, 1968**

ZFMK 5785 Dikume, Rumpi Mts., Cameroon

Hemipenes with two pairs of rotulae and two papillary fields at the base of the sulcal rotulae, up to 8 papillae/field.

***Chamaeleo wiedersheimi* Nieden, 1910**

ZFMK 15283 Mt. Lefo, N.Cameroon

Truncus covered with large calyces that extend over the apex and end abruptly between the asulcal sickle-shaped rotulae. The two sulcal rotulae are more semicircular than the asulcal ones. The margins of the rotulae are finely denticulated. Medially between the sulcal rotulae is one central papillary field with up to 9 papillae.

***Chamaeleo affinis* Rüppell, 1845**

ZFMK 2739 Addis Abeba, Ethiopia

Hemipenes with two pairs of small rotulae. Near the base of each sulcal rotula is a row of extremely long and pointed papillae. The papillae next to the rotulae are the largest, the ones at the end of the row the smallest. Up to 6 papillae/row may be present.

***Chamaeleo goetzei* Tornier, 1899 (Fig. 9)**

ZFMK 30703 and 30705 Ilolo, near Rungwe Mts., Tanzania

Hemipenes clavate, pedicel one third of hemipenislength. The proximal part of the truncus with large calyces, the distal part with small ones that reach high up the median asulcal surface. Sulcal lips well developed and without ornamentation. Apex with two pairs of rotulae, the sulcal rotulae very large, the asulcal rotulae small and oriented transversely. All rotulae are denticulated and are positioned in a large smoothly textured apical area. On the median surface of the sulcal rotulae are two diffuse papillary fields that extend from the distal end of the sulcus over the base of the rotulae well up to the rotulae themselves. In Fig. 9 one sulcal rotula has been folded aside to show one of the papillary fields.

***Chamaeleo fuelleborni* Tornier, 1900**

ZMA 15201 proximity of Kivira, S.E. of Mbeya, Tanzania

The hemipenes look very much like those of *C. goetzei*. The sulcal rotulae are the largest of the four rotulae present. At the median base of these sulcal rotulae are two

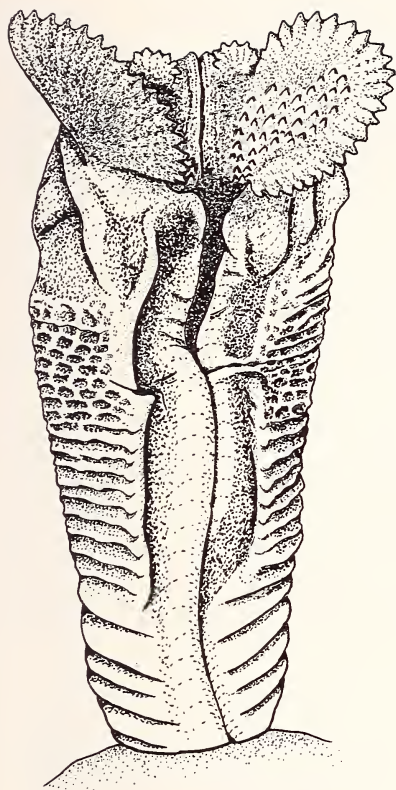


Fig. 9. Hemipenis of *C. goetzei*, sulcal view.

papillary fields as well, but the papillae are more concentrated and do not reach as far up the surface of the rotulae as in *C. goetzei*.

***Chamaeleo tempeli* Tornier 1899**

ZFMK 30706 and 30708 Kigogo, Uzungwe Mts., Tanzania

Four more or less sickle-shaped rotulae are present, the sulcal ones very large, the asulcal ones much smaller. All rotulae are denticulated and positioned in a large smoothly textured apical area. Two papillary fields are present at the median base of the large rotulae, i. e. the papillae do not extend onto the rotulae.

***Chamaeleo laterispinis* Loveridge, 1932**

ZMA 10250 Kigogo, Uzungwe Mts., Tanzania

Hemipenes like those of *C. tempeli* except for 1) the rotulae which are more sickle-shaped and 2) a few additional, scattered papillae next to the papillary fields.

***Chamaeleo werner* Tornier, 1899**

ZFMK 44821 Mufindi, Uzungwe Mts., Tanzania

Hemipenes as in the preceding species, i. e. with four rotulae, the sulcal ones the largest. At the base of each sulcal rotula a large simple papilla is present. Medially between the sulcal rotulae is a diffuse group of small papillae, the asulcal side of the sulcal rotulae is set with very small scattered papillae.

***Chamaeleo tenuis* Matschie, 1892**

ZMH 01848 Amani, Usambara, Tanzania

Hemipenes with two pairs of rotulae. On the inverted hemipenes no additional ornaments could be discerned.

***Chamaeleo fischeri* Reichenow, 1887**

UZM 295 Amani, E.Usambara Mts.; 312 Kwamkoro, E.Usambara Mts. and 322 Muzambai, W.Usambara Mts., Tanzania

Hemipenes stout and clavate, pedicel one fourth of hemipenislength. Truncus with relatively large and deep calyces. Sulcus spermaticus and sulcal lips smooth. The sulcal lips do not continue in a ridge around the apex (= non-capitate). The apex bears four rotulae with serrated margins. The rotulae are of equal size and slightly sickle-shaped. No papillae.

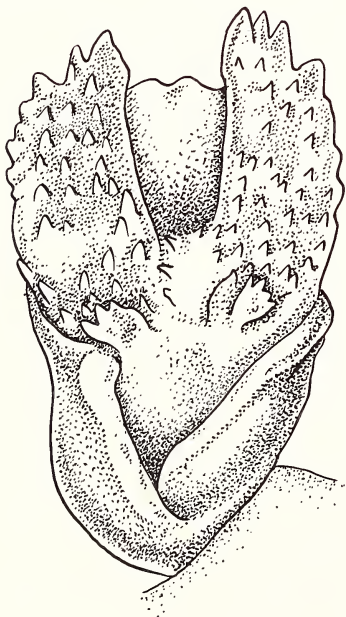


Fig. 10. Hemipenis of *C. mlanjensis*, sulcal view.

***Chamaeleo mlanjensis* Broadley, 1965 (Fig. 10)**

RMB 25380 Chisambo Estate, Mlanje, Malawi

Hemipenes stout and truncated, pedicel short. Truncus with large, shallow and transversely elongated calyces. Apex without rotulae, but characterized by two enormous papillate lobes. The largest papillae are grouped at the distal margin (cf. 'apical wings with scalloped edges', Broadley 1971), the smaller papillae at the centre of the lobes. At the proximal border of each lobe is also a small group of enlarged papillae. The position of these two papillate structures on the apex is similar to that of rotulae. However, they are quite unlike rotulae and much more pliable, like papillae.

***Chamaeleo melanocephalus* (Gray, 1865)**

ZFMK 18417 and 18422 Durban, S.Africa

Hemipenis morphology in accordance with the description of Raw (1976). Four sickle-shaped rotulae are present, the asulcal ones larger than the sulcal ones. The outer margins of the rotulae are denticulated. Between the four rotulae is a median denticulated ridge.

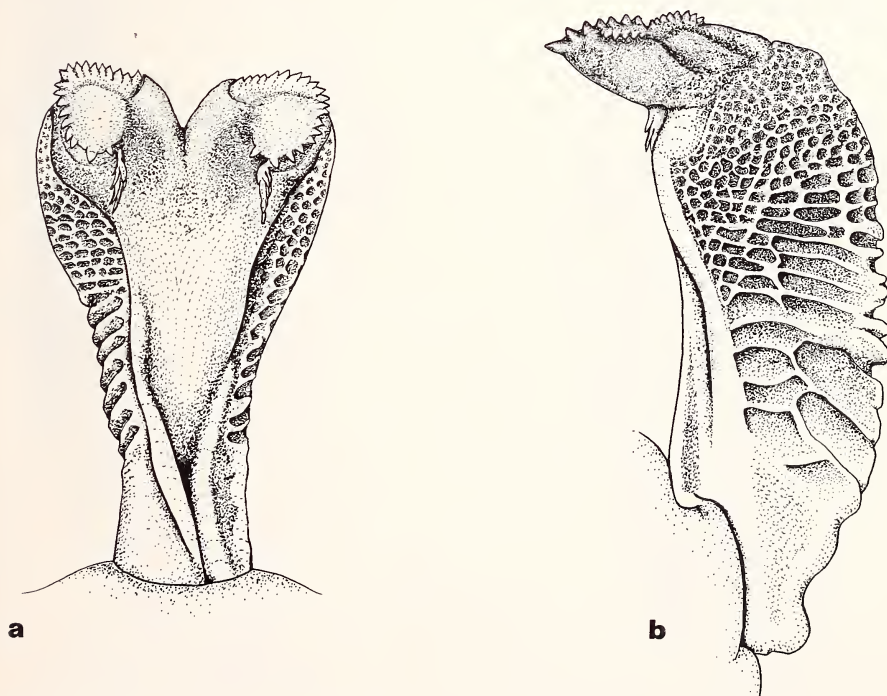


Fig. 11 a & b. Hemipenis of *C. cephalolepis*, a = sulcal view, b = lateral view.

***Chamaeleo tigris* Kuhl, 1820**

ZFMK 26194 Praslin Isld., Seychelles

The hemipenes fit the description of Bourgat & Domergue (1971) except for 1) the shape, that is less elongate, but this may be due to the turgidity at the moment of preservation, 2) the presence of a transverse row of small papillae between the two pairs of elongate papillae ('cornes bifides') and 3) the position of the rotulae ('auricules apicales'), that instead of projecting laterally are positioned on top of the apex.

***Chamaeleo cephalolepis* Günther, 1880 (Fig. 11 a and b)**

ZFMK 29960 and 29963 Grande Comore, Comores

Hemipenes long and clavate, pedicel one fifth of hemipenislength. The calyces on the truncus are large and extend in transverse direction near the pedicel. Distad they become smaller and more hexagonal. Towards the apex the sulcal lips diverge and continue as a ridge that encircles the apex (= capitata). Sulcus spermaticus und sulcal lips without ornamentation. Apex slightly bilobed, each lobe with a broad and somewhat aberrant pedunculus. The outer margin and the distal end of each pedunculus is papillated, i. e. with one major row of papillae (up to 9) and one minor row of papillae (up to 5). These two rows meet proximally and continue in an obliquely orientated denticulate ridge or auricula. At the sulcal base of each pedunculus is a small tuft of superimposed papillae.

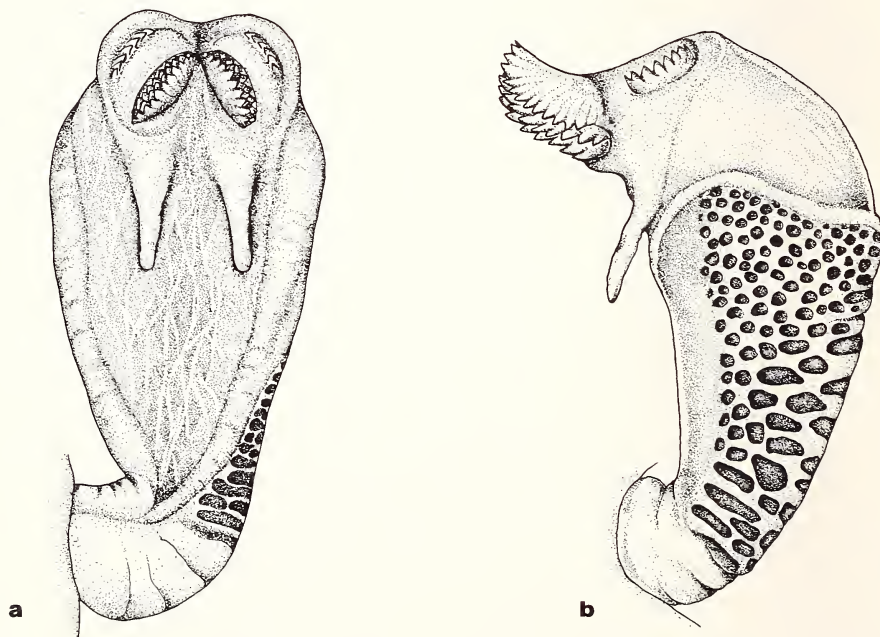


Fig. 12 a & b. Hemipenis of *C. polleni*, a = sulcal view, b = lateral view.

Chamaeleo polleni Peters, 1873 (Fig. 12 a and b)

ZFMK 29917 and 29918 Mayotte, Comores

Hemipenes large and clavate, pedicel one third of hemipenislength. The truncus is covered with rather small calyces that grow even smaller towards the apex. Sulcus, sulcal lips and apex smooth. The capitate apex bears two pedunculi that are fused medially and project over the sulcus. Each pedunculus has three to five parallel rows of papillae at its sulcal und distal margin. At the asulcal side of the pedunculi two slightly raised denticulate auriculae can be observed. Proximally of each pedunculus is an elongate fleshy papilla.

Chamaeleo lateralis Gray, 1831 (Fig. 13)

ZFMK 29984 Tuléar, Madagascar

Hemipenes clavate and capitate, pedicel one fourth of hemipenislength. Truncus calyculate, the calyces growing smaller from the pedicel towards the apex. Apex smooth and characterized by two large and elongate pedunculi that have a papillate sulcal-distal

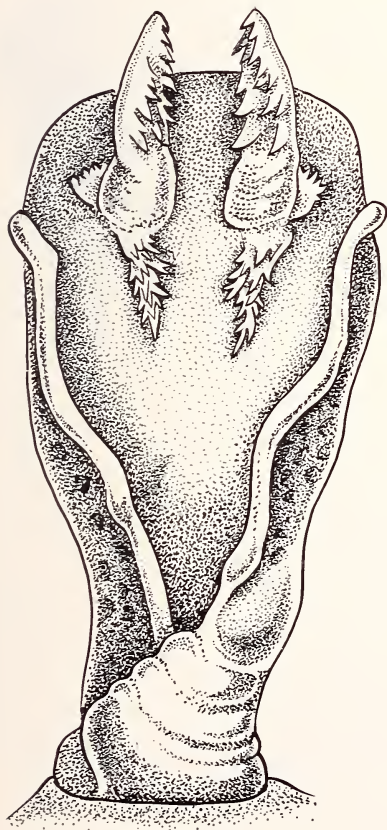


Fig. 13. Hemipenis of *C. lateralis*, sulcal view.

surface (up to 13 papillae). At the base of these pedunculi are 1) at the sulcal side, large tufts of superimposed papillae and 2) at the latero-asulcal side, denticulate auriculae.

***Chamaeleo pardalis* Cuvier, 1829 (Fig. 14 a and b)**

ZFMK 14073 Nosi Bé, N.W.Madagascar and 19333 Maroansetra, N.O.Madagascar

Hemipenes clavate and capitate, pedicel one fourth of hemipenislength. Truncus covered with well developed calyces. Apex slightly bilobed, each lobe ornamented with 1) a stout and curved pedunculus with numerous large pointed papillae at the sulcal-distal surface, 2) a denticulate transverse auricula at the asulcal base of the pedunculus, 3) a large tuft of superimposed papillae at the sulcal base of the pedunculus and 4) four papillae grouped in two pairs near the median midline of the apex. This description corresponds with one given by Bourgat (1969), but as his figures are not particularly clear with regard to the pedunculi, the hemipenis is depicted here again.

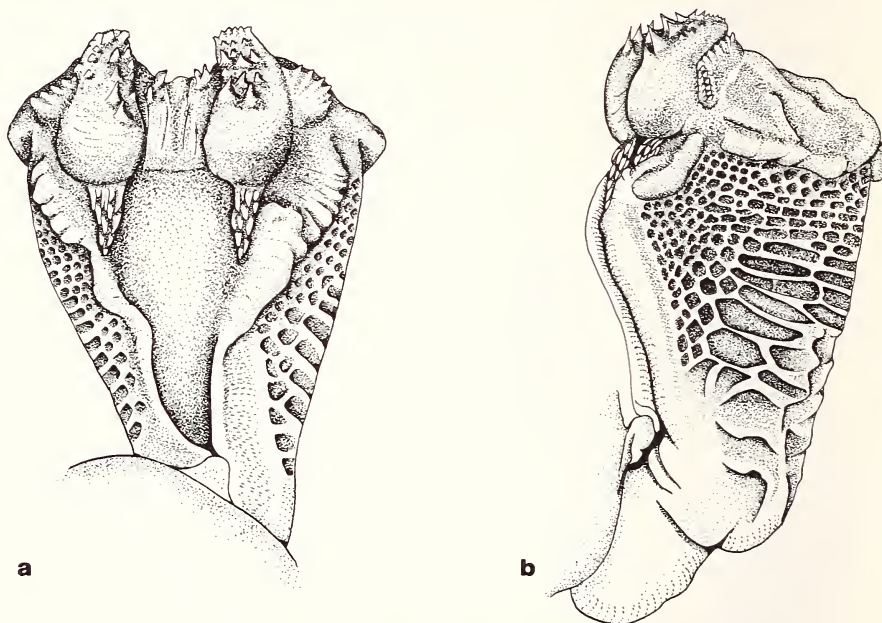


Fig. 14. Hemipenis of *C. pardalis*, a = sulcal view, b = lateral view.

***Chamaeleo oustaleti* Mocquard, 1894**

ZFMK 14546 Majunga, N.W.Madagascar

Hemipenis as described by Bourgat & Brygoo (1968) and very much like those of the previous species. Capitate hemipenis with two stout curved pedunculi, whose sulcal surface bear large pointed papillae. At the asulcal side of each pedunculus is a transverse denticulate auricula. Between these auriculae at the median midline of the apex, is another small, irregularly denticulated ridge. Proximally at the sulcal side of the pedunculi are two elongate and simple papillae.

***Chamaeleo verrucosus* Cuvier, 1829**

ZFMK 17733 and 17734 Tuléar, S.W.Madagascar

Hemipenes like those of *C. oustaleti*, also with two elongate and simple papillae at the sulcal base of the pedunculi. The observation of this ornament in this species and in *C. oustaleti* is contrary to the description of Bourgat & Brygoo (1968), who recorded tufts of superimposed papillae in some of the specimens they examined. However, Brygoo & Domergue (1970 b) report them to be simple as well.*)

***Chamaeleo bifidus* Brongniart, 1800**

ZFMK 20736 Madagascar

Hemipenes with two large pedunculi, at the asulcal side of them two pairs of partially overlapping auriculae. No additional ornaments could be discerned. Next to pedunculi and auriculae Ramanantsoa (1978) recorded the presence of a tuft of superimposed papillae at the sulcal base of each pedunculus and the presence of a single median denticulated ridge ('auricule médio-sommitale, denticulée').

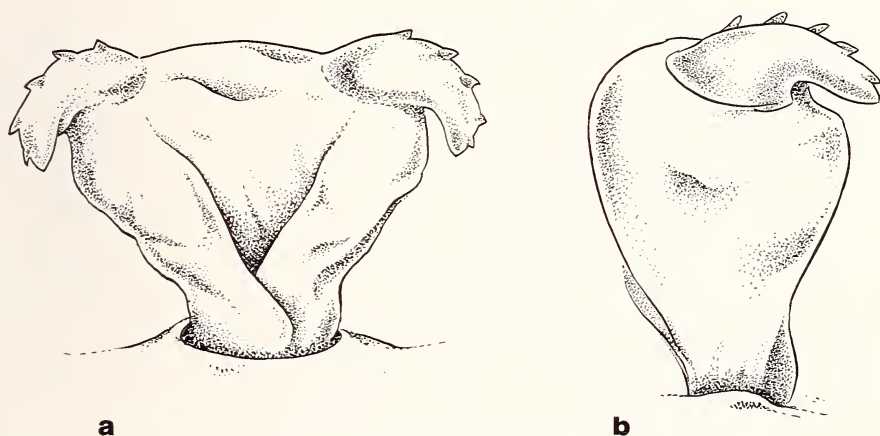


Fig. 15 a & b. Hemipenis of *B. platyceps*, a = sulcal view, b = lateral view.

***Brookesia platyceps* (Günther, 1893) (Fig. 15 a and b)**

RMB 25342 Rud Gorge, Mlanje, Malawi

The hemipenes closely resemble those of *B. p. carri* described by Loveridge (1953). Hemipenes stoutly built and truncated. Pedicel, truncus and apex cannot be distinguished, because calyces and the capitate condition are absent. Two curved apical horns are present, each with a row of papillae.

*) It would be interesting to find out whether this variability in papillate structures correlates with the karyotypic variability within these two species (see section karyology below). An affirmative answer to this question combined with information as to the geographical distribution of the varieties could make a reconsideration of the specific unity of *C. oustaleti* and *C. verrucosus* necessary (cf. also Bourgat 1973).

***Brookesia nchisiensis* Loveridge, 1953**

RMB 6604 Mughesi forest, Misuku Mts., Malawi

Hemipenes stout and truncated, no calyces. Two apical horns with up to 8 papillae, arranged in two rows that converge towards the tip of the horn (cf. Broadley 1971).

***Brookesia brachyura* (Günther, 1893)**

RMB 24348 Matembo Source, Nyika Plateau, Malawi

Hemipenes stout and truncated, no calyces. Two curved apical horns are present, each with up to 6 scattered papillae at the asulcal surface.

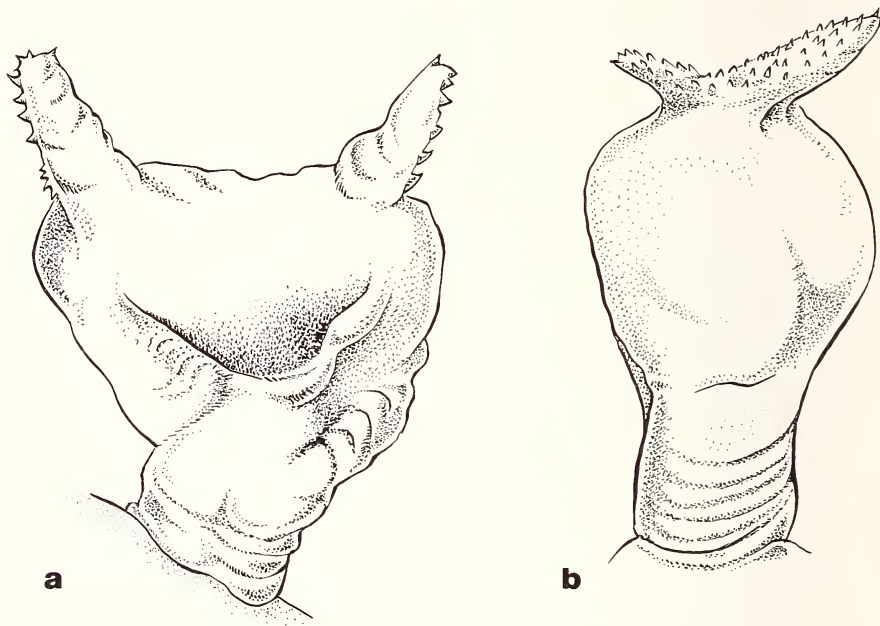


Fig. 16 a & b. Hemipenis of *B. marshalli*, a = sulcal view, b = lateral view.

***Brookesia marshalli* Boulenger, 1906 (Fig. 16 a and b)**

RMB 23230 Vumba Mts., Zimbabwe

Hemipenes with one pair of branched apical horns, the branch orientated towards the asulcal side, approximately half the size of the one that projects towards the sulcal side. The upper surface of these horns is set with numerous small papillae.

***Brookesia spectrum* (Buchholz, 1874)**

ZFMK 1911 Mt. Cameroon, Cameroon and MHNG 1012-5 Foulassi, Cameroon

Hemipenes like those of the previous species, but instead of the apical horns there are two complex apical projections. Each consists of a large denticulate flange (up to 7 den-

ticles), that has on its lateral surface 2 to 3 additional denticles. Directly parallel to this flange is a smaller flange with up to 5 denticles.

Finally we like to comment on several records on hemipenis morphology found in literature. McCann (1949) described the hemipenis of *C. zeylanicus* and Klaver (1981 a) used the differences in hemipenis ornamentation between this form and *C. chamaeleon chamaeleon* in support of an argumentation favouring the specific status of *C. zeylanicus*, as opposed to its generally held subspecific status within the nominal form. The redescription of the hemipenis in this paper shows the observations of McCann on the rotulae arrangement to be erroneous. Both forms mentioned have the same rotulae arrangement, i. e. next to a pair of asulcal rotulae both have three pairs of sulcal rotulae. Consequently this argument in support of a hypothesis of the specific status is invalidated. Not invalidated, however, is the hypothesis of the specific status itself, because of the remaining arguments in favour (cf. Klaver 1981 a: 229) and because other valid species of the *C. chamaeleon* group have the same rotulae arrangement as well.

Domergue (1965) commented briefly on the hemipenes of a number of species, whose hemipenes have unfortunately not been described in detail ever since. The hemipenes of *C. rhinocerus* and *C. labordi* are said to look very much like the ones of *C. lateralis*, *C. oustaleti* and *C. pardalis*. In view of the relationship between these species (cf. Brygoo 1971 and Klaver 1977) and the observations of Bourgat (1971: 239) on the hemipenes of *C. rhinocerus* and *C. angeli* one can safely assume *C. rhinocerus* and *C. labordi*, (and probably *C. antimenae* and *C. monoceras* as well) to have a hemipenis ornamentation with pedunculi and auriculae. As to *C. campani*, often supposed to be related to *C. lateralis*, Domergue (op. cit.) indicated its hemipenis ornamentation to be distinct from that of *C. lateralis*. We confirm this view here, but due to the poor quality of our specimen we cannot give an exact description. We could only establish the presence of two large papillate structures on the apex, rather unlike the pedunculi found in *C. lateralis* which with some imagination remind us of the pedunculi of *C. tuzetae*.

The hemipenes of *C. nasutus* can be distinguished from those of other species, although in certain respects they resemble the ones of *C. bifidus* (Domergue 1965). We do not agree with this observation. *C. bifidus* and allies possess hemipenes with pedunculi and auriculae. According to a picture sent to one of us (CK) by G. Ramanantsoa (in litt.: 28-II-1978) the hemipenes of *C. nasutus* resemble those of, for instance, *C. brevicornis*, i. e. bearing four rotulae and a pair of large bifid papillae. Presumably Domergue mistook the large bifid papillae of *C. nasutus* for the long and slender pedunculi of *C. bifidus*.

According to Domergue (1965) the hemipenes of *C. parsonii* possess four or five hairy protuberances. Brygoo et al. (1971) observed upon the hemipenes of *C. capuroni* that the ornamentation resembles the one of *C. parsonii* very closely. From these observations it is inferred that the hairy protuberances of *C. parsonii* correspond with the four rotulae found in *C. capuroni*. Next to the four rotulae two papillary fields are present, at least in *C. capuroni*, one at the sulcal side of each sulcal rotula.

Finally Domergue (1965) also made some incomplete observations on the hemipenes of *C. brevicornis* and *C. gastrotaenia*. The first species possesses two apical discs, the latter one apparently two lobes with an original ornamentation. Fortunately these meagre observations were amended by Brygoo & Domergue (1970 c), Brygoo et al. (1973) and Brygoo et al. (1970, 1972 b, 1974 a). Next to the apical discs (probably asulcal rotulae) there also proved to be a pair of sulcal rotulae and a pair of large bifid papillae present in *C. brevicornis*. The hemipenis ornamentation in *C. gastrotaenia* is more variable, i. e. next to four smallish rotulae there is either a pair of bifid papillae, a pair of very large simple papillae or no papillae at all. Whether this latter condition is due to seasonal variation, a retained plesiomorph condition or an artefact remains to be seen. An alternative explanation of this variability could be the status of the taxa concerned. The *C. gastrotaenia* subspecies presently known are all small and inconspicuous chameleons with hardly any character to distinguish them. The differences in hemipenis ornamentation may be an indication of their specific status.

HEMIPENEAL CHARACTER EVALUATION

The first problem to be solved is the assessment of the quality of the resemblance of the hemipenis characters, i. e. to examine whether or not they can be considered homologous and, if so, at what level they constitute a synapomorphy. Chameleons as a group are generally considered a sistergroup of the Agamidae with which they share various supposedly synapomorphous characters as, for instance, acrodont dentition, absence of caudal autotomy (Camp 1923) and the presence of a ramus duodenalis of the caecal artery (Henke 1975). Unfortunately the absence of data concerning the hemipenis morphology in Agamidae forestalls an outgroup comparison and thus a hemipeneal character evaluation at this level. Occasional observations on hemipenes of preserved specimens present in the collection of the ZFMK reveal that the apices in different Agamidae are slightly or moderately bilobed, but without any ornamentation comparable to that found in the Chamaeleonidae. There are, however, ways to arrive at some assessment of chameleon hemipenis characters, viz. by outgroup comparison at a higher level and by outgroup comparison at a lower level, i. e. within the Chamaeleonidae themselves. An outgroup comparison at a higher level than that of the immediate sistergroup allows the calyces to be characterized. Calyces are not only found abundantly in most saurian families, but in many ophidian families as well. Such a wide distribution of a character in so many distantly related groups leads to the conclusion that calyces are a plesiomorph character within the Squamata, unless we are willing to accept a rather too prolific amount of convergence. It follows that the absence of calyces or rather the smooth mesial surface of the hemipenes in *Brookesia* be considered an autapomorphy of this group, assuming the remaining, unexamined species to lack calyces as well. As to the apical ornamentation it is postulated here that the different forms of ornamentation as found within the Chamaeleonidae have evolved de novo within this group and that the relative plesio- and apomorphy must be assessed at intra-familial level.

The most general and widespread type of apical ornamentation present within the Chamaeleonidae is the one consisting of four rotulae, that are eventually accompanied by papillae or papillate structures. General and widespread does not only refer to the absolute number of species possessing four rotulae, but also to the occurrence of this trait in species that are, considered on the basis of other evidence, related in various degrees. Species possessing this type of apical ornamentation occur in Africa, south of the Sahara, Madagascar and the Seychelles. All species possessing a four rotulae type of hemipenis ornamentation belong to the genus *Chamaeleo*. The remaining *Chamaeleo* species have either a rotulae ornamentation with more than four rotulae (the *C. chamaeleon*-group only) or an ornamentation characterized by two pedunculi and two auriculae, that are eventually accompanied by papillae or papillate structures (a group of chameleons restricted to Madagascar and the Comores). The two latter types of ornamentation are found in far less species than the first one discussed. Until now no species of *Chamaeleo* is known to lack an apical ornamentation.

If we restrict ourselves for the time being to the genus *Chamaeleo* we postulate that the similarity in ornamentation, i. e. the possession of four rotulae be considered characteristic of or synapomorphous for a large and heterogeneous group of chameleons and to reflect affinity at a general level. The four rotulae cannot, therefore, be used to assess the relationship of the different species within this group, because at that level they must be considered a symplesiomorphy. These latter relationships can, as will be demonstrated below, be inferred from the differences and similarities in rotulae development, in rotulae form and in the additional apical ornaments, viz. papillae and papillate structures. The other two types of apical ornamentation, viz. the multi-rotulae type and the pedunculi-auriculae type are considered to be derived secondarily and independently. We found this character transformation sequence on a morphological hypothesis concerning the homology of the various apical ornaments, that can be inferred from correspondence in position and composition and from intermediate forms.

It is not hard to conceive that asulcal rotulae and auriculae are homologous, as may be inferred from their position on the apex and their similarity in appearance. As we have seen the difference between a denticulated flange or disc and a denticulated ridge was not sufficient enough to prevent French authors to consider these two characters identical and to coin them with the same term 'auricule'. We differentiate them, however, precisely because of their relative morphological dissimilarity and attribute their relative morphological similarity and position to homology. Auriculae as we perceive them are always found in combination with pedunculi, whereas asulcal rotulae are always found in combination with sulcal rotulae. This observation begs the question whether pedunculi can be regarded homologous with sulcal rotulae. We think this indeed to be the case, both ornaments are present in pairs at a sulcal position on the apex and may have developed from relatively undifferentiated ornaments, similar to the ones found in *C. mlanjensis*. There are two arguments in support of this homology hypothesis. First, there are the peculiar pedunculi of *C. polleni* and *C. cephalolepis* with their flattish shape and each showing two to five parallel rows of papillae at their sulcal

and distal margin (see Figs. 11 a, b and 12 a, b). One can imagine that a bulging development combined with a simultaneous rotulae-like development at the same location gave rise to this condition. Subsequent evolution may then have resulted in more lobe-like and finally stalk-like pedunculi as observed in other Malagasy species. The "disques apicaux pediculés" of *C. brevicornis*, *C. malthe* and *C. peyrierasi* may also fit in this scheme, but we do not want to pursue this speculation because we found the rotulae of *C. brevicornis* to look like perfectly normal rotulae. Second, the sulcal pair of apical ornaments, be they either pedunculi or rotulae, exhibit during evolution a similar major development. Pedunculi develop into large and conspicuous sulcal ornaments with numerous rows of papillae; sulcal rotulae may likewise become large (cf. *C. goetzei*, Fig. 9) or may increase in number (cf. the *C. chamaeleon*-group). The parallel rows of papillae on the pedunculi of *C. polleni* may even be homologous with the parallel rotulae of the sulcal rotulae groups in the species of the *C. chamaeleon*-group.

The papillate structures that generally accompany the pair of major sulcal ornaments are mostly paired as well and positioned more or less sulcal-medially of these ornaments. These papillate structures may consist either of papillary fields, papillary rows, large bifid papillae or large simple papillae in the case of rotulae or of simple, bifid, or tufts of superimposed papillae in the case of pedunculi. It is hypothesized that these papillate structures are homologous and reflect the different stages in a development from a relatively undifferentiated condition with many small papillae scattered over the apex (cf. *C. mlanjensis* and *C. hoehnelii*, Böhme & Klaver 1980) towards a relatively differentiated condition with papillae either grouped in fields, rows, tufts or in pairs of large bifid or large simple papillae. Other minor papillate structures, either single or paired, may be found on the apex especially in a distal-medial position. These papillate ornaments are, however, much more variable and, therefore, hard to homologize. Summarizing this hypothesis: pedunculi are homologous with sulcal rotulae, auriculae are homologous with asulcal rotulae, and simple, bifid and tufts of superimposed papillae found at the sulcal base of the pedunculi are homologous with other papillate structures such as bifid papillae, papillary fields, etc. found at the base of sulcal rotulae.

An alternative hypothesis can be formulated in which pedunculi are not considered homologous with sulcal rotulae but with large papillate structures found in several Malagasy species. When describing the hemipenes of *C. tigris* Bourgat & Domergue (1971: 239) stated in relation to the two pairs of remarkable elongate bifid papillae: "Les cornes; leur situation correspond à celle des lobes (1) connus dans la majorité des espèces, lobes dont elles semblent être les homologues". In a footnote they explain what they consider a lobe: "(1) = pédoncule, in Bourgat 1969, p. 56", which in this case is indeed synonymous to pedunculus and not to pedicel. Similarly when describing the hemipenes of *C. gastrotænia marojezensis* Brygoo et al. (1970: 274) observe upon the unique "lobes filiformes hypertrophiés" that they "occupent la place des lobes communs chez la plupart des Caméléons". If one searches the literature on hemipenes morphology present at the time one finds that pedunculi were frequently referred to as

"lobes" (cf. *C. balteatus*, Brygoo & Domergue 1969 c; *C. belalandaensis*, Brygoo & Domergue 1970 b and *C. angeli*, Bourgat 1971). Apart from these two observations on the location of large papillate structures on the apex the French authors did not pursue the homology question any further in their subsequent papers. Presently we know that the location of most conspicuous papillate structures, large and small, is at the base of either sulcal rotulae or pedunculi. The nature of the two structures mentioned is, in our opinion, clearly, papillate and their resemblance with pedunculi superficial at best. Their location on the apex more likely corresponds with that of other papillate structures instead of that of the pedunculi in other Malagasy species. Moreover, additional data, e. g. the pedunculi structure of *C. polleni* and *C. cephalolepis* makes homology of pedunculi and sulcal rotulae more plausible, whereas in case of the alternative hypothesis sulcal rotulae are not accounted for. Therefore we do not think the alternative hypothesis plausible, we only mentioned it here to acknowledge that we did not fail to record the possibility.

The apical ornamentation of the *Brookesia* species differs from the ones of the *Chamaeleo* species in that it is much simpler and less variable. Either a pair of horns or a pair of crests is present, only occasionally accompanied by additional papillate structures. The external appearance of horns and crests is suggestive, i. e. horns remind us of pedunculi and crests remind us of auriculae or even rotulae. Although these possible homologies cannot be ruled out a priori there are no additional arguments to support the idea that the superficial resemblance can indeed be ascribed to homology. On the contrary, the papillae present on the horns are on the 'wrong' or asulcal side and, moreover, the dual aspect of the apical ornamentation forestalls to establish with the help of the relative position with which of the apical ornaments found in *Chamaeleo* horns and crests are most likely to be homologous. The two denticulated flanges found in *B. spectrum* might suggest a four rotulae condition, but the two flanges are so close to each other that a further differentiation of a single ornament is more likely. The compound crest-like arrangement of *B. spectrum* might correspond to the compound horn-like arrangement of *B. marshalli*, in spite of the crests of Malagasy species. Fresh everted material is necessary to check this view.

Horns and crests might be homologous and represent two independent developments. We think the ornaments in *Brookesia* have been evolved independently from the ones found in *Chamaeleo* and to constitute synapomorphies in their own right. This view is endorsed by the development of a smooth mesial surface in the hemipenes of *Brookesia* species, that clearly sets them apart from the *Chamaeleo* species.

The above information and argumentation can be summarized in a cladogram (Fig. 17) in which groups of species are characterized by synapomorphous hemipenis characters. It is tentatively assumed that species whose hemipenis morphology is still unknown fit into the cladogram, i. e. do not possess a hemipenis ornamentation that cannot be ascribed to either type of ornamentation discussed. In view of the number of species whose hemipenis morphology is already known and the assumed affinity between some of these species and the species whose hemipenes morphology is unknown we think it not too bold a contention.

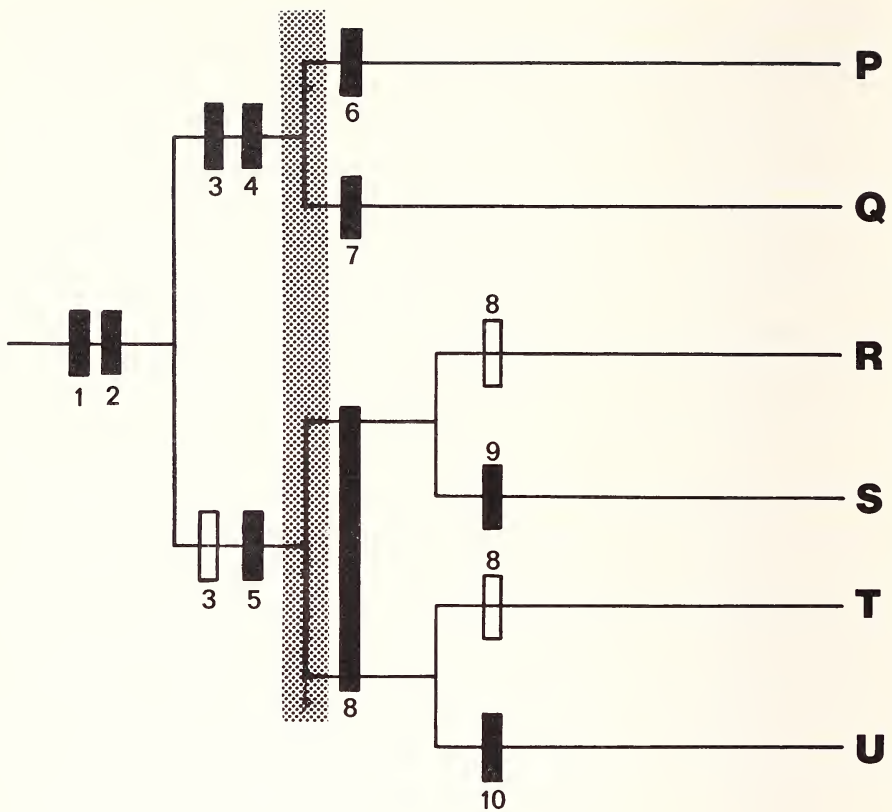


Fig. 17. Cladogram based on hemipenis characters. Black rectangles: synapomorphies, open rectangles: symplesiomorphies. 1: chameleonid manus and pedes, 2: extensile tongue, 3: calyces present (open) or absent (black), 4: dual aspect of apical ornamentation, 5: quadruple aspect of apical ornamentation, 6: crests, 7: horns, 8: four rotulae ornamentation, 9: pedunculi and auricular ornamentation, 10: multi-rotulae ornamentation. Shading: separation of Madagascar and Africa. P: Malagasy *Brookesia* species; Q: African *Brookesia* species; R: Malagasy and Seychelles *Chamaeleo* species: *C. brevicornis* c. s., *C. gastrotaenia* c. s., *C. nasutus* c. s., *C. parsonii* c. s. and *C. tigris*; S: Malagasy and Comores *Chamaeleo* species: *C. bifidus* c. s., *C. lateralis* c. s., *C. polleni* c. s., *C. pardalis* c. s. and *C. rhinocerus* c. s.; T: African *Chamaeleo* species except those of *C. chameleon* c. s. (= U).

Although it is not possible to define the Chamaeleonidae with the help of hemipenis characters (it may even prove to be impossible), the family can be defined easily and unambiguously by other apomorph characters, that are unequally shared by all members. These characters are the highly modified manus and pedes and the extensile tongue (characters 1 and 2 in Fig. 17). It is surprising, therefore, that in literature numerous apomorph characters are listed that are supposed to characterize the family.

Although many of these characters may indeed be derived and even unique within the Chamaeleonidae they are seldom shared by all members of the family. A recent example is Estes (1983), who lists a. o. the following shared derived character states of the family: "... skull high, narrow with parietals and squamosals extending posterodorsally into a casque ..." and "... nasals excluded from the naris (sic) by maxilla (sic) and prefrontals ...". Although this may apply to many chameleon species there are various species in which the parietals and consequently the skull are more or less broad and flat and squamosals not extending posterodorsally, viz. *B. platyceps* (Frank 1951), *B. spectrum* (Werner 1902 b) and *B. superciliaris* (Siebenrock 1893). Moreover, in *B. superciliaris* the nasals clearly border the external nares dorsally. So in spite of promising words in the foreword of his paper Estes (op. cit.) stuck to tradition, i. e. generalized observations on certain characters in one or several species and presented an enumeration of these characters that are supposed to be characteristic for chameleons at large, thus completely ignoring available conflicting data concerning these characters in other species.

The pygmy chameleons (genus *Brookesia*) and the ordinary chameleons (genus *Chamaeleo*) are characterized by the synapomorphies 4 (dual aspect of the apical ornamentation) and 5 (quadruple aspect of the apical ornamentation) respectively. The monophyly of the *Brookesia*'s is further evidenced by synapomorphy 3, the absence of calyces. The genus *Brookesia* can be subdivided into two subgroups, viz. the Malagasy species (P) characterized by crests (6) and the African species (Q) characterized by horns (7). The subdivision corresponds with the former subdivision of the pygmy chameleons into two genera, viz. *Brookesia* Gray, 1865 and *Rhampholeon* Günther, 1874.

In the genus *Chamaeleo* four subgroups can be recognized, viz. two groups characterized by the possession of four rotulae, one group characterized by more than four rotulae and one group characterized by pedunculi and auriculae. We have argued that the possession of four rotulae (8) is characteristic of a large and heterogeneous group of chameleons. The subdivision of this group into two subgroups (R and T, Fig. 17) is validated by arguments concerning the relationship between species within the respective subgroups that will be discussed in subsequent sections on external morphology, lungmorphology and zoogeography. Group R constitutes the Malagasy-Seychelles branch, group T the continental Africa branch of species of the four rotulae group. Within group R a further differentiation can be made with the help of papillate structures. *C. capuroni* and *C. parsonii* and probably the related *C. globifer* and *C. oshaughnessyi*, have next to each sulcal rotula a papillary field. *C. gastrotaenia andringitraensis* and *C. g. guillaumeti* possess next to the sulcal rotulae two large bifid papillae. This character is also found in *C. peyrierasi*, *C. tigris*, *C. nasutus*, *C. cucullatus*, *C. brevicornis* and *C. malthe* and is likely to be found as well in the related species *C. fallax*, *C. gallus*, *C. boettgeri*, *C. guibei*, *C. linotus*, *C. furcifer* and *C. tsaratananensis* whose hemipenis morphology is still unknown. *C. g. marojezensis* has instead of the bifid papillae two very large simple papillae next to each sulcal rotula, whereas *C. g. gastrotaenia* seems to lack large papillate structures. This latter condition

probably represents a retained plesiomorph condition as compared with the apomorph papillate condition.

Within group T a similar differentiation can be made by means of the papillate structures. The plesiomorph non-papillate condition is found in *C. pumilus* and allies, *C. fischeri*, *C. tenuis*, *C. melleri*, *C. ellioti*, *C. arabicus* and *C. namaquensis*. The composition of this group clearly demonstrates that this is a paraphyletic group. The relationship of *C. arabicus* and *C. namaquensis*, for instance, lies definitely with the *C. chamaeleon* group (see sections karyology and lungmorphology) that is characterized by a synapomorphous multi-rotulae ornamentation. *C. arabicus* and *C. namaquensis* are the only members of this group that have retained the plesiomorph four rotulae configuration. Other species that can be expected to lack papillate structures are *C. adolfifriederici*, *C. carpenteri*, *C. spinosus*, *C. uthmoelleri* and *C. xenorhinus*. Small papillae scattered over the apex are found in *C. mlanjensis* and *C. hoehnellii*. Rows of papillae at the base of each sulcal rotula are found in *C. affinis* and *C. kinetensis*. Scattered papillae or rows of papillae are likely to be found in the related *C. chapini*, *C. rudis*, *C. schoutedeni* and *C. schubotzi*. Simple large papillae at the basis of the sulcal rotulae are found in *C. oweni* and *C. werneri*. Papillary fields are found in *C. bitaeniatus*, *C. jacksonii*, *C. cristatus*, *C. johnstoni*, *C. montium*, *C. feae*, *C. camerunensis*, *C. eisentrauti*, *C. quadricornis* and *C. wiedersheimi* and can be expected in *C. pfefferi* and *C. deremensis*. Papillary fields are also found in *C. goetzei*, *C. fuelleborni*, *C. laterispinis* and *C. tempeli*, but then in a combination with very large sulcal rotulae that are characteristic of this group. *C. incornutus* is likely to have the same apical ornamentation. Similar derived papillate structures in group R and T are considered parallel developments in the two independent branches within the four rotulae group.

The species of group S are characterized by a synapomorphous apical ornamentation consisting of pedunculi and auriculae (9). Variation in this group concerns pedunculi development, viz. lobe-like, stalk-like and cusped in, for instance, *C. tuzetae*, *C. pardalis* and *C. bifidus* respectively and auriculae development, viz. simple, compound and doubled in, for instance, *C. tuzetae*, *C. oustaleti* and *C. bifidus* respectively. Papillate structures at the sulcal base of the pedunculi may be absent (*C. balteatus* and *C. campani*), simple (*C. polleni*, *C. oustaleti*, *C. verrucosus* and *C. willsii*), bifid (*C. minor*, *C. petteri* and *C. tuzetae*), or tufted (*C. angeli*, *C. belalandaensis*, *C. bifidus*, *C. cephalolepis*, *C. lateralis* and *C. pardalis*). Tufted papillae are likely to be found in *C. antimena*, *C. labordi*, *C. monoceras* and *C. rhinoceras* as well, considering their affinity to *C. angeli*. Most species of this group have previously been recognized to be related on account of external morphological and karyological data (cf. Brygoo 1971; Klaver 1977 and 1981 b). *C. bifidus*, *C. minor*, *C. willsii* and *C. balteatus* are included in this group for the first time.

No additional papillate structures are found in species of group U; they are, however, characterized by a multi-rotulae arrangement (10), that is supposed to have been derived from the original four rotulae condition. Within this clearly monophyletic group (*C. chamaeleon*-group) an arrangement of six (*C. calyptratus*), eight (*C. chamaeleon*, *C. africanus*, *C. dilepis*, *C. laevigatus*, *C. quilensis*, *C. zeylanicus* and *C. gracilis*) and even

ten rotulae (*C. senegalensis* and *C. calcaricarens*) can be distinguished. A similar multi-rotulae arrangement is to be expected in the related *C. anchietae* and *C. monachus*.

COMPARISON WITH OTHER CHARACTER SETS

In this paragraph our hypothesis concerning the relative plesiomorphy and apomorphy of hemipenis characters is tested against similar transformation series in other character sets, notably karyology and lungmorphology. Data on osteological characters are scarce but sufficiently distributed among species to permit some general conclusions. External morphological data will not be discussed within the framework of a transformation series, but the congruence and especially the incongruence of the grouping of species by these characters as compared with that by hemipenis characters is commented on.

External morphology

In the Chamaeleonidae external characters are, as in most other groups of organisms, still the most widely employed characters to distinguish species and to establish their relationships. The most recent comprehensive studies on external morphology of chameleons are those of Hillenius (1959) and Brygoo (1971, 1978). Both authors distinguish especially within the genus *Chamaeleo* groups of species, consisting of species that are assumed to be more closely related to one another than to any member of other species groups. Hillenius (1963) also considers the relationship between various groups of species. The informal subdivision of *Chamaeleo* by the respective authors diverges somewhat, though not essentially, partly because Hillenius does not restrict himself to Malagasy species, as does Brygoo, but includes African and Eurasian species as well; and partly because Hillenius (1959, 1963), unlike Brygoo, restricts himself to the genus *Chamaeleo*, i. e. does not include the *Brookesia* species into his considerations. It is beyond the scope of this section to analyse and discuss external morphological characters in detail and at length. It suffices for the present purpose to make a comparison of the results of their study with the results of the study of hemipenis characters and to comment on the assumed affinity of several Malagasy and African species in particular.

The groups of species as defined with the help of external morphological characters are in many cases congruent with the ones that can be distinguished with the help of hemipenis characters, e. g. the *C. chamaeleon*-group, the *C. goetzei*-group, the *C. cristatus*-group etc. In other cases the outcome of the study of hemipenis characters amends the subdivision based on external characters in that it either establishes the affinity of species whose relationship was still unclear, e. g. *C. tigris*; or unites groups of species into more inclusive groups, e. g. *C. nasutus* cum suis (c. s.), *C. gastrotaenia* c. s., *C. brevicornis* c. s. and *C. tigris* are characterized by elongate bifid papillae and *C. oustaleti* c. s., *C. rhinoceratus* c. s., *C. bifidus* c. s. as well as *C. cephalolepis* and *C.*

polleni characterized by pedunculi and auriculae. In still other cases hemipenis characters lead like other characters (see other sections below) to conclusions that are contrary to the ones based on external morphological characters. One such case is the assumed affinity of *C. bifidus* c. s. of Madagascar with *C. fischeri* c. s. of Africa (Hillenius 1959, 1963). The species of the respective geographical areas resemble each other, notably in the possession of a rostral protuberance, but hemipenis ornamentation refute the hypothesis of relationship. *C. bifidus* c. s. have a hemipenis ornamentation that is very different from the one possessed by *C. fischeri* c. s. (pedunculi and auriculae versus four rotulae) and, what is more, the apomorph hemipenis characters relate *C. bifidus* c. s. to other Malagasy species instead. Any closer relationship of *C. fischeri* c. s. to other African species remains unclear, because of the relatively plesiomorph condition of their hemipenis ornamentation.

Why should in this case resemblance in hemipenis characters be considered to reflect phylogenetic relationship whereas resemblance in external morphological characters does not? The answer lies, we think, not so much in the difference of quality of the charactersets employed as in the difference in the methods employed. As has been demonstrated above we make a comprehensive analysis of hemipenis characters and formulate preliminary hypotheses concerning homology and relative apomorphy of these characters. Subsequently hypotheses concerning phylogenetic relationship are formulated. These hypotheses are then compared with the results of similar procedures concerning other character sets (see subsequent sections) which leads either to corroboration or refutation. Hillenius (1959, 1963) and Brygoo (1971, 1978) on the other hand do not analyse external morphological characters nor do they put forward hypotheses concerning phylogenetic relationship in chameleons in general. Instead they compare species and group them according to their similarity to give a short (probably too short to do them justice) characterization. As is to be expected this phenetic approach sometimes leads to false estimates of relationship and fails to establish existing relationships. Just as 'dissimilarity' cannot simply be regarded as evidence of the absence of phylogenetic relationship, 'similarity' cannot simply be regarded as evidence of the presence of phylogenetic relationship. Not the degree of (dis)similarity is of primary importance, but the kind of (dis)similarity. We think the case of *C. bifidus* and *C. fischeri* c. s. illustrates the inherent shortcoming of this methodology. Synapomorphous hemipenis characters relate *C. bifidus* c. s. to other Malagasy chameleons instead to the continental *C. fischeri* c. s. Consequently the resemblance in external morphology has to be regarded as either a symplesiomorphy or a parallel development, or our hypotheses concerning hemipenis characters are erroneous. When the data discussed so far are evaluated in the context of the whole group (Chamaeleonidae) and not in this particular case only we feel that the latter possibility is quite improbable. Moreover, we think our view is corroborated when additional character sets are considered. We like to stress that we do not imply to say that our view of hemipenis character evolution and consequently our view of chameleon phylogeny is the only right and possible one. We only think our postulates and hypotheses are such that a most plausible and parsimonious explanation of hemipenis characters is given that is,

simultaneously, congruent with plausible and parsimonious explanations of data from other character sets. This results in the best estimate of chameleon relationship possible at present. From the phylogenetic relationship of *C. bifidus* and other Malagasy species as evidenced by hemipenis morphology and the absence of a closer affinity of these species to *C. fischeri* follows that the possession of similar characters as rostral protuberances has to be either a symplesiomorphy or parallelism. In this instance we think it safe to opt for the latter possibility since the presence of this character appears to be apomorphous as compared with the assumed plesiomorph condition in which rostral protuberances are absent.

Analogous to the *C. bifidus*—*C. fischeri* case Hillenius (1959, 1963) related the species of the Malagasy *C. rhinocerus*-group to the Central African *C. carpenteri* and *C. xenorhinus*, and the species of the Malagasy *C. nasutus* group to the East African *C. spinosus* and *C. tenuis*. Although we do not know the hemipenis morphology of *C. carpenteri* and *C. xenorhinus* we expect it to be very different from the one found in *C. rhinocerus* c. s. These latter species, too, have a highly derived hemipenis ornamentation that relates them to other Malagasy species (e. g. *C. oustaleti* c. s.) and which appears to be the result of a long and independent evolutionary process on Madagascar (see also Klaver 1977, 1981 b). The relationship assumed by Hillenius is, therefore, refuted, which is not surprising for it was never firmly substantiated. The hemipenes of *C. nasutus* are characterized by two pairs of elongate papillae. This apomorph character is shared by several other Malagasy species only, that are therefore thought to be related. *C. tenuis* does not possess this character and, consequently, we doubt that any resemblance in external morphology between *C. nasutus* and *C. tenuis* reflects close relationship. Whether these two latter cases of similarity in external morphology are to be ascribed to parallelism as well remains to be seen, as the possibility of symplesiomorphy cannot be ruled out.

Resemblance of chameleon species from Madagascar and East Africa are to our opinion the result of the fact that both chameleon fauna's consist of descendants of the same ancestral stock which was subdivided by the separation of Madagascar and Africa (see section Zoogeography and Böhme MS). Symplesiomorphies, e. g. four rotulae ornamentation and resemblance in gross external morphology (cf. Werner 1911 a); parallel developments, e. g. papillate structures and rostral protuberances; and apomorph characters unique of species of the respective geographical areas, e. g. pedunculi, auriculae and large bifid papillae are all compatible with this evolutionary history of the group. The above arguments combined with similar ones in subsequent sections are the justification to subdivide the four rotulae group into an African branch and a Malagasy branch.

Karyology

The karyotypes of 40 chameleon species are known from the studies of Bourgat (1971 a, 1971 b, 1972, 1973), Brink (1957), De Smet (1981), Matthey (1957, 1961), Matthey & Brink (1956, 1960), Robinson (1971) and Wright & Broadley (1973). Originally two dif-

ferent patterns were distinguished, viz. a discontinuous karyotype with a clear separation between macro- and micro-chromosomes and a continuous karyotype with less or no clear separation between macro- and micro-chromosomes. The chromosome number of the discontinuous karyotypes is the highest, $2n = 36 = 12M + 24m$; that of the continuous karyotypes the lowest, $2n = 20 = 18M + 2m$. Due to the geographical distribution the discontinuous type was called 'continental' (= African) and the continuous type 'insular' (= Madagascan and Comoran). However, the correlation between karyotype and geographical area is not complete, since some Malagasy species have a continental karyotype and some African species an insular one. Subsequent studies revealed intermediate karyotypes to exist, although a distinction can be retained between continuous karyotypes with a high number of macro-chromosomes and a small number of micro-chromosomes, and discontinuous karyotypes with a small number of macro-chromosomes and a high number of micro-chromosomes separated by a clear sizegap. Moreover, the continental-insular distinction was corrected, i.e. changed into a correlation between discontinuous karyotypes and a savannah-like distribution and between continuous karyotypes and a montane distribution (Matthey 1970). This correlation was subsequently changed or rather reversed by Bourgat (1973) at least as far as Malagasy species were concerned. Discontinuous karyotypes are found in the east of Madagascar in humid forests, continuous karyotypes correspond to the west of Madagascar, to bush, savannah and caducous forest.

Matthey (e. g. 1960) observed that the karyotype $2n = 36 = 12M + 24m$ is not only found in the Chamaeleonidae but also in other lizard groups, e. g. Iguanidae, Agamidae, Amphisbaenidae and Gerrhosaurinae. He concluded that this resemblance could not indicate close relationship and, dismissing the possibility of a joint retained primitive character, he assumed it to be the result of convergence. As a consequence of this and also in view of his ideas concerning the various processes active during chromosome evolution (centric fusion and centric fission) he considered the discontinuous karyotype to have evolved by an increase of the chromosome number from the continuous one. Surprisingly this implied an opposite direction of chromosome evolution as has been envisaged by him in the other lizard families mentioned! On the basis of the same observations, i. e. similar karyotypes in different families, Gorman (1973) arrived at the opposite conclusion. He considered $2n = 36 = 12M + 24m$ the primitive karyotype and the other ones derived, Bourgat (1973) agreed with this view and considered the $12M + 24m$ karyotype in the Chamaeleonidae the primitive one and the other karyotypes, especially the continuous ones derived. Hillenius (1963) tried to reconcile the karyotypic information with his hypotheses about primitive characters and chameleons. Ironically the species Hillenius considered primitive have a karyotype that is primitive neither according to Matthey's view nor according to Gorman's and Bourgat's view of chromosome evolution. He had to take pains to fit the karyological facts via speculative karyological processes into his hypotheses, not only because Matthey's view were (with hindsight) incorrect, but his own ideas as well (cf. Klaver 1981 b). We think the best thing to do is to try not to explain away the variability in karyotypes within the Chamaeleonidae with the help of simple assumptions about undoubtedly

complicated karyological processes. Without the purpose to belittle the contributions of the cytogeneticists mentioned, our present knowledge of chameleon karyotypes is still very limited and superficial. The karyotypic data available consist of the number and shape of the chromosomes in less than a third of the species known. These non-differentially stained karyotypes do not permit the recognition of identical karyotypes of different species as is possible with banding methods. This, in turn, makes hypotheses about possible processes of chromosomal evolution hazardous. However, more general considerations as to pattern are very well possible.

We disagree with Matthey's conclusion that the karyotype the different lizard families have in common is the result of convergence. His conclusion resulted from a questionable hypothesis of chromosome evolution in chameleons and the failure to appreciate the relative nature of the notions primitive and evolved. Gorman (1973) summarized karyotypic data of some 300 species and thought the high incidence of the $12M + 24m$ karyotype among the various lizard groups sufficient, apart from his process hypothesizing, to consider this karyotype the primitive one. We agree with him and many subsequent authors that the karyotype $12M + 24m$ represents a symplesiomorphy that indeed does not indicate close relationship. It does reflect, however, a distant common ancestor and a synapomorphy at a higher hierarchical level.

Table 1 summarizes the karyotypes of the Chamaeleonidae presently known arranged according to the total number of chromosomes. The *Chamaeleo* species with the plesiomorph karyotype $12M + 24m$ all possess a more or less plesiomorph hemipenis ornamentation with four rotulae and either without additional papillate structures (*C. fischeri* and *C. gastrotaenia*) or with papillary fields (the remaining species). Malagasy species with a discontinuous but derived karyotype have, as far as is known, also a partially derived hemipenis ornamentation, i.e. next to the four rotulae they possess instead of papillary fields a pair of elongate bifid papillae (*C. brevicornis* and *C. nasutus*). *C. campani* and *C. willsii* are exceptional in that they have a discontinuous though intermediate karyotype, but a hemipenis ornamentation that is quite different from that of two previous species. The ornamentation resembles the one of the remaining Malagasy and Comoran species, all of which have a highly derived continuous karyotype, and consists of pedunculi, auriculae and either a pair of simple or bifid papillae or a pair of tufts of papillae. It would be interesting to obtain more pertinent information about the hemipenis ornamentation of *C. campani* because that may prove to be intermediate and give some insight in the origin of pedunculi. Similarly the karyological study of the nearest relatives of *C. willsii*, viz. *C. bifidus*, *C. minor* and *C. petteri* may reveal them to possess intermediate karyotypes as well, that in turn may facilitate hypothesizing concerning karyotypes. When the karyotypes of these latter species are the same as the one of *C. willsii* or perhaps even belonging to the continuous type the hypothesis of close affinity between *C. fischeri* and *C. bifidus* c.s. is disproved once again. Moreover, Hillenius (1963) considers the $12M + 24m$ karyotype found in *C. parsonii* c.s. and *C. fischeri* c.s. an indication of affinity between the species of the *C. parsonii*-group and the *C. bifidus*-group. A similar karyotype found in the *C. cristatus*-group would, however, lead to a grouping of species that Hillenius thought not

Table 1: Known karyotypes of chameleons, arranged according to total number of chromosomes. *C. oustaleti* and *C. verrucosus* exhibit chromosomal variability.

2n=	composition	Malagasy species (incl. Comoran)	African species
36	12M+24m	<i>C. gastrotaenia</i> <i>C. globifer</i> <i>C. oshaughnessyi</i> <i>B. stumpffi</i>	<i>C. cristatus</i> <i>C. fischeri</i> <i>C. johnstoni</i> <i>C. wiedersheimi</i>
34	12M+22m 16M+18m	<i>C. gallus</i> <i>C. nasutus</i>	<i>C. pumilus</i>
32	12M+20m 18M+14m	<i>B. nasus</i> <i>C. brevicornis</i>	
28	12M+16m 14M+14m 24M+4m	<i>C. boettgeri</i> <i>C. willsii</i> <i>C. cephalolepis</i>	
26	12M+14m	<i>C. campani</i>	
24	12M+12m		<i>C. africanus</i> <i>C. chamaeleon</i> <i>C. dilepis</i> <i>C. namaquensis</i> <i>C. senegalensis</i> <i>C. zeylanicus</i>
	20M+4m	<i>C. antimena</i> <i>C. lateralis</i> <i>C. polleni</i> <i>C. labordi</i>	<i>C. biteaniatus</i> <i>C. hoehnelii</i> <i>C. jacksonii</i>
22	22M+2m 20M+2m 18M+4m	<i>C. oustaleti</i> <i>C. pardalis</i> <i>C. verrucosus</i> <i>C. angeli</i> <i>C. oustaleti</i> <i>C. rhinocerotus</i> <i>C. verrucosus</i>	
20	18M+2m		<i>B. marshalli</i> <i>B. spectrum</i>

to be "taxonomically plausible" and is therefore regarded a convergence. We argue that *C. fischeri* is not related to the species of the *C. bifidus*-group and that the 12M + 24m karyotype found in various Malagasy and African species is not the result of convergence but is a retained i.e. symplesiomorph karyotypic condition.

In Africa the variety of intermediate karyotypes is or rather appears to be much less, but we find the karyological synapomorphies in congruence with the hemipenis synapomorphies in the *C. chamaeleon*-group. An exception is *C. namaquensis* that re-

tained the plesiomorph four rotulae condition but possesses the synapomorphous karyotype of the group. *C. pumilus* has a plesiomorph hemipenis ornamentation, a condition that is mirrored by its karyotype that differs only slightly from the original karyotype. Exceptional are the species of the *C. bitaeniatus*-group, they are characterized by a highly derived continuous karyotype but their hemipenis ornamentation appears to be rather plesiomorph, except for the additional papillate structures. The karyotype $2n = 24 = 20M + 4m$ is also found in several Malagasy species, but as both these species and *C. bitaeniatus* c.s. are related to quite different species because of synapomorphies such as hemipenis ornamentation and lung septation this karyological resemblance has to be ascribed to parallelism. It would be very instructive to have information about the karyotypes of *C. goetzei* and allies because we suspect them to have karyotypes that are intermediate to the ones of *C. cristatus* c.s. and *C. bitaeniatus* c.s. The data of Table 1 also illustrate that the correlation between discontinuous karyotypes and savannah distribution does not hold for African species since *C. quadricornis* and allies occur in a montane forest habitat despite their discontinuous karyotype.

The karyotypes of the four *Brookesia* species differ markedly. The Malagasy species have plesiomorph discontinuous karyotypes, the African species highly derived continuous karyotypes. Unfortunately little can be said about correlation with hemipenis ornamentation, except for the bold contention that horns are apomorph in relation to crests. We can conclude that there is a fairly good congruence between the polarity of the karyological and the hemipeneal transformation series and the grouping of species that results from the respective series.

Osteology

Osteological studies of chameleons are not only few in number but also limited to a small number of species. The studies of Vrolijk (1827), Siebenrock (1893) and Werner (1902 b) deal with the complete skeleton of *C. chamaeleon*, *B. superciliaris* and *B. spectrum* respectively. Parker (1881), Boulenger (1886), Fineman (1939, 1941), Brock (1940), Engelbrecht (1951), Frank (1951), Visser (1972) and Rieppel (1981) discuss only the skull morphology of *C. chamaeleon*, *C. pumilus*, *C. ellioti*, *C. melleri* and *B. platyceps*. Miscellaneous observations on the osteology of these and a few other species are recorded by, for instance, Bauer (1886), Werner (op. cit.) and Methuen & Hewitt (1914). As a result we are quite ignorant of the osteological characteristics of the majority of chamaeleon species and thus of the variation of these characters that would otherwise have permitted a character evaluation. The osteological data known are, however, sufficiently distributed among species to permit some general inferences as to character polarity.

In *B. superciliaris* the external naris is bordered by three bones, viz. the nasal, the maxilla and the prefrontal (Siebenrock 1893). This condition is typical for lizards in general and is generally considered plesiomorph. In *Chamaeleo* species the nasal is excluded from the dorsal margin of the external naris, the naris is bordered by the maxilla and

the prefrontal only. The nasal borders a prefrontal fontanella together with either the frontal and the prefrontal (*C. pumilus*) or the prefrontal and the maxilla (*C. chamaeleon* c. s., *C. melleri* etc., Rieppel 1981 a. o.). In *B. spectrum* and *B. platyceps* an intermediate condition is observed, i. e. the fontanella and the external naris are not completely separated by the excrescences of the prefrontal and the maxilla. This results in one large aperture that is narrowed mesially and bordered by the nasal, the frontal, the prefrontal and the maxilla (Werner 1902 b and Frank 1951). The incomplete subdivision of the enlarged external naris apertures is not due to insufficient ossification of a juvenile skull as Rieppel (1981) suggested. Rieppel cogently argued, on the other hand, that the condition found in *B. platyceps*, *B. spectrum* and the *Chamaeleo* species has been derived from a condition similar to the one found in *B. superciliaris* (relatively small nasal apertures and no fontanellae).

In *C. gastrotaenia*, *C. hoehnelii*, *C. namaquensis*, *C. nasutus*, *C. pumilus* and *B. marshalli*, *B. platyceps*, *B. spectrum* and *B. superciliaris* the orbitae are bordered dorsally by three bones, viz. the prefrontal, the frontal and the postorbital (Klaver 1981 b and personal observations). This condition that is also found in lizards of other families (Anguidae, Varanidae, Iguanidae etc.) is generally considered plesiomorph. The condition in which the frontal is excluded from the orbital margin by a contact of the prefrontal and the postorbital is thought to be derived. This condition is also found in various lizard families, e. g. Agamidae, Anniellidae, Helodermatidae, Pygopodidae and Chamaeleonidae (*C. chamaeleon*, *C. dilepis*, *C. gracilis*, *C. jacksonii* and *C. melleri*, Romer 1956 and Rieppel 1980). The frontal has receded even further in *C. pardalis* resulting in a second set of fontanellae in the dermal roof of the skull (personal observation). These frontal fontanellae are bordered medially by the frontal and laterally by the orbital margin that consists of the prefrontal and the postorbital. Incidentally, the development of superciliary crests in *Brookesia* species is of course a highly derived condition despite the plesiomorph configuration of the component bones.

A third marked difference in skull architecture is found in the parietal region. *B. superciliaris* has a broad flat parietal with two latero-ventral processes (Siebenrock 1893). The processes meet the postero-dorsal processes of the squamosals with which they border the upper temporal fossae posteriorly. This condition corresponds to the one found in other lizards (Brock 1940 and Methuen & Hewitt 1914). In *B. spectrum* the parietal is also broad and flat but without the latero-ventral processes. The posterior margin of the upper temporal fossae is entirely made up by the ascending postero-dorsal processes of the squamosals (Werner 1902 b). In *Chamaeleo* we find still other parietal structures. *C. pumilus* has a parietal that is broad but not flat, it extends upwards postero-dorsally to form a casque with a curved median crest. Besides, there are two latero-ventral processes that descend to meet the ascending squamosal processes halfway the posterior margin of the upper temporal fossae (Parker 1881, Brock 1940 and Engelbrecht 1951). In *C. chamaeleon* the parietal is a very narrow upward curving bone that constitutes the median or parietal crest. There are no parietal processes but the squamosals extend upwards towards the tip of the parietal where they almost meet. This latter type of casque construction has been found in various other species and was,

therefore, often thought to be characteristic of chameleons at large. In *C. senegalensis*, *C. pardalis* and *C. namaquensis* the parietal is flattened medio-laterally and the squamosals actually meet behind the parietal. In *C. cristatus*, *C. montium* and *C. parsonii* the parietal is similar, though not extending postero-dorsally and flattened dorso-ventrally at the posterior end, so the squamosals do not meet. Despite this variation and the considerable variation in casque height the parietal always seems to be a narrow bone without latero-ventral processes in *Chamaeleo* species (excluding *C. pumilus*). It thus appears that in the Chamaeleonidae there is a fully plesiomorph parietal condition (*B. superciliaris*: broad, flat parietal with processes), a fully apomorph parietal condition (probably in the majority of *Chamaeleo* species: narrow casque forming parietal without processes) and two intermediate parietal conditions (*B. spectrum*: broad, flat parietal without processes and exactly the reverse condition in *C. pumilus*: broad, casque forming parietal with processes). Consequently Rieppel's contention that there are only two basic types of casque construction in chameleons is a simplification that was probably caused by his apparent ignorance of Werner's (1902 b) revealing paper on the skeleton of *B. spectrum*. *B. spectrum* and also *B. platyceps* have a parietal that is clearly to be distinguished from the one found in *Chamaeleo* species.

In these three examples the Malagasy *Brookesia* species possess the plesiomorph character states. The African *Brookesia* species are plesiomorph as to the orbital bordering bones, but are intermediate in case of the other two characters. *Chamaeleo* species generally have the most apomorph character states, i. e. species which are derived in other character sets (hemipenis ornamentation and karyotype) are also apomorph in osteological characters. Several chameleon species that are relatively plesiomorph in respect to hemipenis and karyological characters (*pumilus*, *gastrotaenia*, *namaquensis*) possess also relatively plesiomorph or intermediate osteological character states. It thus appears that the direction of character transformation in the osteological character set is the same as the one in the karyological and hemipeneal character sets.

Lung-morphology

The lung-morphology of the majority of chameleon species is known from the studies of Wiedersheim (1886), Milani (1894), Beddard (1907), Werner (1911 a), Methuen and Hewitt (1914), Broman (1942), Klaver (1973, 1977, 1979, 1981 b) and Böhme & Klaver (1980). In the older literature two types of lungs were distinguished, viz. simple lungs without septation or diverticula (*C. pumilus*) and lungs with a more differentiated structure, i. e. with septation and diverticula (*C. chamaeleon* a. o. see Klaver 1973). This simple dichotomy was proved wrong when a far more elaborate variation in lungstructure was established within the Chamaeleonidae (Klaver 1973, 1977, 1979, 1981 b). As to the septation five discrete types could be distinguished. Absence of septation was established in *Brookesia* species (Werner 1911 a and Klaver 1979), but the lungs of *C. pumilus* were, contrary to prior opinion, clearly septated with numerous small septa on the dorsal and ventral wall of the lungs. The four other types of septation are characterized by either one, two or three large septa that run longitudinally through the lumen of the lung from the orifice of the bronchus towards posterior. In one type the

septa end freely in the lumen, in the three other types the septa continue and curve ventrad to meet the ventral wall of the lung (for more details see Klaver 1981 b). The different types of septation are not randomly distributed among species but are often clearly correlated with groups of related species.

As to the diverticula no such regularity is found. Although species (-groups) are often characterized by shape and number of diverticula, there are exceptions as well, i. e. the lungs of closely related species show a very different diverticula composition. *C. pumilus* is not the only chameleon to lack diverticula, the lungs of *C. cephalolepis*, *C. guibei*, *C. fallax*, *C. spinosus*, *C. tigris*, *C. tsaratananensis* and *C. xenorhinus* are also non-diverticulate. Moreover, of the twenty *Brookesia* species examined only four African species were found to possess diverticula, viz. *B. brachyura*, *B. brevicaudata*, *B. kerstenii* and *B. nchisiensis*. The absence of diverticula within the Chamaeleonidae is considered a symplesiomorphy that correlates with symplesiomorph character states in other character sets. An exception is *C. cephalolepis* that has a derived hemipenis ornamentation and karyotype. Most species of the genus *Chamaeleo* and a few species of *Brookesia* have diverticula, that is thought to be a derived character (Klaver 1981 b).

Klaver (op. cit.) discussed a transformation series concerning the different septa arrangements within the Chamaeleonidae. Absence of septa in all *Brookesia* species is considered a symplesiomorphy. The various septation types arose by subsequent evolution from the non-septated lungtype. It was argued that the septa arrangement with numerous small septa on the dorsal and ventral wall of the lungs was the first to evolve. This septation type is found in all *Chamaeleo* species of Madagascar, the Comores and the Seychelles and in a number of African species, viz. *C. fischeri*, *C. mlanjensis*, *C. pumilus*, *C. spinosus*, *C. tenuis* and *C. xenorhinus*. This character distribution among species correlates with that of the relatively plesiomorph four rotulae ornamentation (without additional papillate structures) in African species and all four rotulae and pedunculi-auriculae types of ornamentation in the Malagasy, Comoran and Seychelles species. The explanation of the occurrence of this type of lung septation in species of the various geographical areas is the same as the one explaining the occurrence of the four rotulae condition in species of Madagascar, Africa and the Seychelles. Absence of close relationship between species of Madagascar and Africa, combined with the established relationship between the species of Madagascar lead to the conclusion that resemblance is the result of the fact that both chameleon fauna's consist of descendants of the same ancestral stock that was subdivided by the separation of Madagascar and Africa. Klaver (1981 b) erroneously stressed that the resemblance is the result of parallelism, but it will be clear that the four rotulae ornamentation as well as the multi-septa arrangement are symplesiomorphies. Parallelism does occur of course, e. g. similar papillate ornaments and rostral protuberances.

The synapomorph pedunculi-auriculae ornamentation of Malagasy species is not correlated with a different type of septation, all Malagasy species have the same type of septation. Conversely, African species with a four rotulae ornamentation accompanied by papillate structures did develop septa arrangements of their own. In the species of the *C. bitaeniatus*-group one small and one large septum is connected with the ventral

wall of the lung. This synapomorphy is congruent with the derived continuous karyotype of this group. In the species of the *C. goetzei*-group and the *C. cristatus*-group and in *C. oweni* and *C. johnstoni* two large septa are connected with the ventral wall of the lung. The species of the *C. goetzei*-group can be distinguished from the other species by the large sulcal rotulae that characterize them. *C. oweni* and *C. johnstoni* can be included in the *C. cristatus*-group on account of their lung septation, their hemipenis ornamentation (lack of papillary fields as compared with the other species) must be considered a retained plesiomorph condition.

C. melleri has an autapomorph lung septation with three septa connected with the ventral wall of the lung. Unfortunately the relatively plesiomorph hemipenis ornamentation furnishes no clues as to the nearest relative of this apparently isolated species.

The septation type that is characteristic of the species of the *C. chamaeleon*-group (two large septa ending freely in the lumen of the lung) is correlated with the multi-rotulae ornamentation and a derived discontinuous karyotype. *C. namaquensis* clearly belongs to this group as karyotype (Robinson 1979) and lung-morphology (Klaver 1977) indicate. Like *C. arabicus* it retained, however, a plesiomorph four rotulae ornamentation.

We can conclude that the two lung characters discussed, viz. diverticula and especially septation show a regular modification in extant taxa indicating a direction of modification sequence that is congruent with the polarity of other characters in the same taxa.

In addition to the observations on lung characters Klaver (1973, 1977, 1981 b), and before him Germershausen (1913), discussed the presence of an inflatable gular pouch connected with the ventral wall of the larynx in species of the genus *Chamaeleo*. Their observations concord except for *C. lateralis* in which Germershausen found a gular pouch to be present whereas Klaver did not. The presence of a gular pouch was established in species of the *C. chamaeleon*-group, viz. *C. africanus*, *C. anchietae*, *C. calypttratus*, *C. chamaeleon*, *C. dilepis*, *C. gracilis*, *C. laevigatus*, *C. monachus*, *C. namaquensis*, *C. quilensis*, *C. senegalensis* and *C. zeylanicus*, and the *C. oustaleti*-group, viz. *C. oustaleti*, *C. verrucosus*, *C. tuzetae*, *C. antimena*, *C. labordi* and *C. rhinocerotus*. In the last three species mentioned the gular pouch is only indicated. Apart from these two groups of species a gular pouch was also found in four comparatively unrelated species, viz. *C. pumilus*, *C. melleri*, *C. goetzei* and *C. cucullatus*. *C. pumilus* is relatively plesiomorph in its hemipenis morphology, karyology and lungmorphology. The other three species mentioned are, as far as is known, at least partially more derived. Other species of the *C. goetzei*-group and the *C. cucullatus*-group do not have a gular pouch.

The absence of a gular pouch in *Brookesia* species (Klaver 1979) and in most of the relatively plesiomorph *Chamaeleo* species indicates that the presence of the gular pouch is a synapomorphy within the genus *Chamaeleo*. A few relatively plesiomorph species have a gular pouch, but most of the species related to them do not. Truly derived species do have a gular pouch although the congruence with other derived characters in the *C. oustaleti*-group is not as complete as in the *C. chamaeleon*-group.

Summarizing this section, in which the various character sets are compared, we think we can safely conclude that there is a good congruence in the direction of transformation sequence of hemipeneal, karyological, lung-morphological and osteological characters and in the grouping of taxa that result from the respective series. Of course, there is not an exact congruence, some synapomorph characters are more or less inclusive than their congruent ones. However, the general congruence in polarity of the various character sets in approximately the same taxa makes the basic assumptions as to each transformation series and the series themselves seem right.

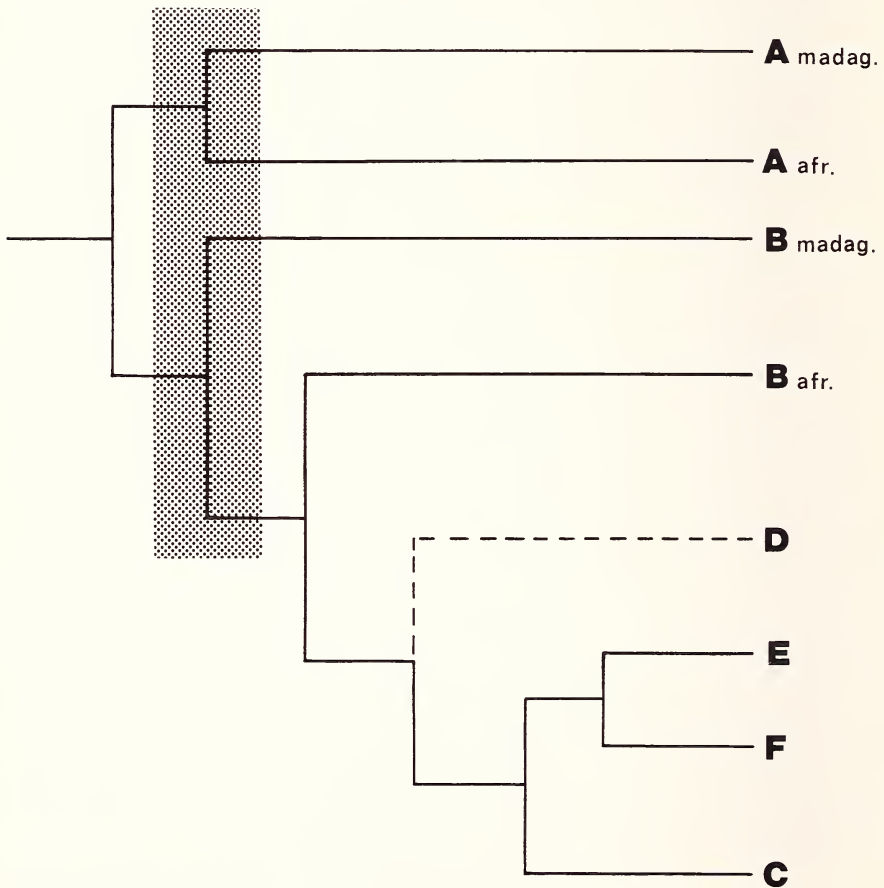


Fig. 18. Phylogram based on lung-septation characters, changed after Klaver (1981 b). A: no septation, B: numerous small septa on dorsal and ventral wall of the lung, C: free-ending longitudinal septa, D: three septa connected with the ventral wall of the lung, E: two large septa connected with the ventral wall of the lung, F: one small and one large septum connected with the ventral wall of the lung. Shading: separation of Madagascar and Africa.

COMPARISON OF PHYLOGENIES

Klaver (1981 b, Fig. 27) proposed a phylogeny of chameleons based on lung septation characters. This phylogeny is reproduced here (Fig. 18), though it is changed according to the text of Klaver's paper, i. e. lungtypes A and B are split into an African and a Malagasy branch. When we compare this phylogeny with the one based on hemipenis ornamentation (Fig. 17) we find them to match quite well.

The synapomorph characters of *Brookesia* species (dual aspect of the apex ornamentation, lack of calyces, crests (group P) and horns (Q, see Fig. 17), are not correlated with synapomorph lungcharacters but with the symplesiomorph non-septated type of lung (Aafr. and Amadag., Fig. 18).

The Malagasy branch of the lungtype with numerous small septa on the dorsal and ventral wall of the lung (Bmadag.) corresponds with the groups R and S, i. e. the differentiation in hemipenis ornamentation is not mirrored by the lungseptation. As lungtype Bmadag. can at this level be regarded a symplesiomorphy the grouping of Fig. 17 (R and S) is to be preferred as this is (partly) based on synapomorphies.

Lungtype C, characteristic of the species of the *C. chamaeleon*-group, corresponds exactly with the multi-rotulae ornamentation of this group (U).

As to the remaining African species the most significant difference is the grouping of lungtype Bafr., D, E and F in one group (T) of the hemipenis-cladogram. According to Fig. 18, however, groups D, E and F are closer to group C than to group Bafr. Group T is characterized by symplesiomorphous hemipenis characters, whereas C, D, E and F are characterized by relatively synapomorph lungseptation characters as compared with group Bafr. Groups C, D, E and F all have lungtypes with large septa that run lengthwise through the lumen of the lung and that, in congruence with the transformation series, are thought to have been derived from lungseptation type Bafr. Therefore, the grouping of Fig. 18 is preferable to that of Fig. 17. Moreover, the uncertain position of *C. melleri* (D) can be clarified by placing *C. melleri* closer to the species of groups E and F. The reason for this is that in the lungs of several species of these groups, viz. *C. affinis*, *C. ellioti*, *C. schubotzi* and *C. wiedersheimi* a third small ventral septum has been recorded that might be homologous with the third large septum of *C. melleri* (Klaver 1977 and Böhme & Klaver 1980). Consequently all species with septa connected with the ventral wall of the lung are united into one subgroup. This grouping of D, E and F correlates with, for instance, the presence of the synapomorphy annulated horns in species of all groups, viz. *C. melleri* (D), *C. deremensis*, *C. fuelleborni*, *C. johnstoni*, *C. montium*, *C. oweni*, *C. pfefferi*, *C. quadricornis* and *C. werneri* (E), *C. jacksonii* (F). Combining this information on synapomorphies of the two character sets results in a phylogeny of chameleons as depicted in Fig. 19. When we compare the data from the section on transformation series we often find them to support this phylogeny, e. g. the 12M + 12m karyotype characteristic of group C and the 20M + 4m characteristic (?) of group F. It should be noted that not all groups are defined by synapomorphies, e. g. one of the branches of Bmadag. (corresponding with group R of Fig. 17) and Bafr.

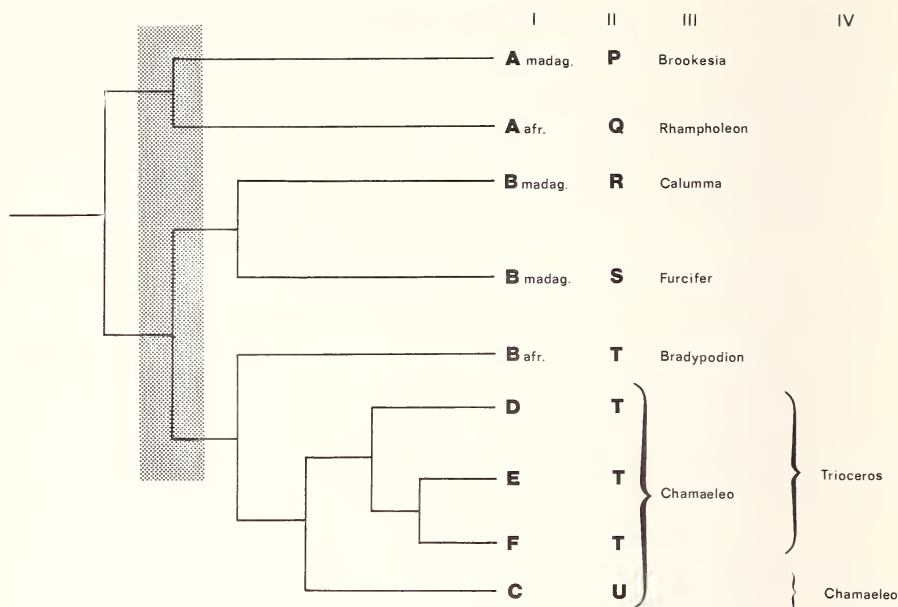


Fig. 19. Phylogeny of chameleons. I = lung-septation types (cf. Fig. 18 for explanation), II = hemipenis ornamentation types (cf. Fig. 17 for explanation), III = genera, IV = subgenera of chameleons, for explanation see text. Shading: separation of Madagascar and Africa.

Future studies are needed to improve this situation by looking for synapomorphies in other character sets or by re-evaluating already studied character sets, notably external morphology in the context of this phylogenetic scheme.

ZOOGEOGRAPHY

To explain the peculiar distribution pattern resulting from the assumed relationship between various Malagasy and African species of *Chamaeleo* Hillenius (1959, 1963) had to postulate quite a bit of migrating to and fro between Madagascar and Africa. The affinity of the species concerned (*C. bifidus-fischeri*, *C. rhinocerotus-xenorhinus* and *C. nasutus-tenuis*) and the migration hypotheses have already been questioned by Klaver (1977, 1981 b) on account of lung-morphological data. In this paper the argumentation as to the absence of close relationship between African and Malagasy species is endorsed by hemipeneal and karyological characters and it is shown that the relationship of at least the Malagasy species concerned lies clearly with other Malagasy species.

The distribution of species of the two oldest monophyletic groups, viz. *Brookesia* species and *Chamaeleo* species characterized by a four rotulae ornamentation and a

lung septation with numerous small septa on the dorsal and ventral wall of the lungs, in Africa and Madagascar is not the result of dispersal across the Mozambique Channel by rafting but of the fact that both faunas consist of descendants of the same ancestral stock. The ancestral stock was subdivided in an African and a Malagasy branch by the formation of the Mozambique Channel (cf. Brygoo 1978). The separate branches evolved and diversified in the separate geographical areas which led to endemism (there are no species that occur in both Africa and Madagascar) and sometimes to parallel developments. Another part of the similarity of Malagasy and African species is caused by symplesiomorph characters.

The separation of Madagascar and Africa by the opening up of the Mozambique Channel has been denied, i. e. assuming the geological fixity of landmasses (Milot 1972) or explained by the origin of a geosyncline between otherwise stable landmasses (Förster 1975). Recently, however, evidence has been accumulated indicating the separation to be caused by sea-floor spreading shifting the Malagasy landmass from the Kenya-Tanzanian coast southwards to its present position during the Cretaceous (Rabinowitz et al. 1983).

The distribution of the species of the *C. chamaeleon*-group also makes the dispersal by rafting hypotheses unlikely. Species of this group range all over Africa, southern Europe, the Near East, the Arabian peninsula, India, and adjacent islands such as Sicily, Crete, Samos, Rhodos, Cyprus, Sokotra, Zanzibar and Ceylon. Why a member of this widely dispersed group would not have succeeded to reach an island as large as Madagascar is hard to understand. When the origination of species of this group from the African branch of ancestral chameleons (Fig. 17 and Fig. 19) is accepted, however, it becomes clear that species of the *C. chamaeleon*-group (U) could not reach Madagascar because they evolved in Africa, after the Mozambique Channel had opened up.

The distribution of *C. cephalolepis* and *C. polleni* on the Comores and of *C. tigris* on the Seychelles, and their relationship to Malagasy species does also fit in this pattern of separation of Madagascar and Africa. *C. cephalolepis* and *C. polleni* are thought to be related to Malagasy species, notably those of the *C. oustaleti*-group (Hillenius 1959, 1963; Brygoo 1971 and Klaver 1981 b). Their hemipenis morphology described in this paper confirms this view. It is, therefore, assumed that the Comores and Madagascar were in contact quite a long time after they separated from Africa (Klaver, op. cit.). The ancestors of *C. cephalolepis*, *C. polleni* and the species of the *C. oustaleti*-group evolved on the Comores-Malagasy landmass and were subsequently separated when the Comores and Madagascar split up.

Hillenius (1959) tentatively assumed *C. tigris* to be related to species of the African *C. pumilus*-group and the *C. bitaeniatus*-group. On account of this Cheke (1984) had to conclude that *C. tigris* is "... the only Seychelles lizard of an apparently directly African origin." The rest of the lizard fauna of the Seychelles is typically Malagasy or consists of African elements that have reached the islands via Madagascar or the Comores. The hemipenis ornamentation of *C. tigris* clearly relates this species to Malagasy

chameleons instead of African ones. This makes *C. tigris* to fit in the general zoogeographical pattern of the Seychelles. The occurrence of *C. tigris* on the Seychelles does not require waif dispersal from Madagascar as an explanation. The Seychelles Bank has a remarkable continental structure, i. e. it is underlain by continental crust and the islands can be regarded a micro-continent that was isolated by the opening up of the Indian Ocean. The Seychelles are probably existing separately from Africa, Madagascar and India since the early Tertiary (Braithwaite 1984). Prior to this separation the ancestors of *C. tigris* and its Malagasy relatives had established on the land-mass of which the present Seychelles and Madagascar were a part. It, thus, appears that the distribution of chameleons in Africa, Madagascar, the Comores and the Seychelles can be explained concisely by the same major geological processes that were active during the end of Mesozoic and the beginning of the Cenozoic.

CLASSIFICATION

In this article we reviewed and evaluated the available information of various character sets bearing upon the majority of chameleon species and proposed a phylogeny of chameleons in which groups and subgroups are defined as far as possible by shared derived characters. Despite imperfections in this phylogeny we think it is justified to propose a new (provisional) classification of chameleons in accordance with the phylogeny discussed. Not only does this improve our insight into the phylogenetic relationships of chameleons, it also makes explicit the main problems for future studies to focus on.

The classification of chameleons has changed comparatively little in the past. Once chameleons were considered an order, viz. Rhipitoglossa, but have long since been treated as a monophyletic group of family rank within the infra-order Iguania. For a detailed familial diagnosis see Dowling & Duellman (1978), Klaver (1981 a) and Estes (1983). The intra-familial classification of chameleons has changed more often, i. e. more than the currently recognized two genera *Brookesia* and *Chamaeleo* have been proposed (e. g. see Klaver 1979 a. o.). However, these subdivisions have proved to be untenable and had to be abandoned. Notorious in this respect are the recurrent attempts to classify the South African species of the *C. pumilus*-group in a separate genus. The last attempt was made by Raw (1976) who based the resurrection of the genus *Bradypodion* Fitzinger, 1843 almost exclusively on data concerning the South African species, thereby neglecting available conflicting data concerning other chameleon species. It is, therefore, no surprise that none of his "generic characters" proved to be unique or characteristic for the genus proposed! We adopt and like to emphasize the view that was already expressed by Mertens (1966) that a reclassification of chameleons in more genera "... wäre nur auf Grund einer morphologischen Untersuchung sämtlicher Chamäleon-Arten möglich" (emphasis in original). For details of the intra-familial nomenclatorial history see the synonymy-chresonymy list of Mertens (op. cit.).

The first phylogenetic branching within the Chamaeleonidae (see Fig. 19) is considered subfamilial. Two subfamilies are recognized, viz. **Brookesiinae** and **Chamaeleoninae**, that are characterized by the absence of calyces and a dual apical ornamentation and the presence of calyces and a quadruple apical ornamentation respectively.

The Brookesiinae are subdivided in two groups, viz. a Malagasy and an African group. This subdivision coincides with the geographical separation of the species of the respective groups by the formation of the Mozambique Channel at the end of the Cretaceous. The Malagasy species are classified in the genus *Brookesia* Gray, 1865 and are characterized by the presence of crests on the hemipenis apex; the African species are classified in the genus *Rampholeon* Günther, 1874 and are characterized by the presence of horns on the hemipenis apex. Moreover, various osteological and karyological characters are presumably characteristic of the respective groups (see the relevant sections above).

The Chamaeleoninae can likewise be subdivided in a Malagasy and an African group. These groups cannot be defined by apomorph characters but their justification can be inferred from the same geographical separation caused by the formation of the Mozambique Channel as in the case of the Brookesiinae. Moreover, this point of view is supported by preliminary results of an immunological study in which the immunological distance between the Malagasy *C. pardalis* and the African *C. dilepis* is calculated at approximately 60 mybp. (Hofmann, pers. comm.).

Within the Malagasy group two subgroups can be distinguished, of which one can be defined by the synapomorphic pedunculi and auriculae on the hemipenis apex. This group is treated here as a genus for which the oldest available name is *Furcifer* Fitzinger, 1843, the type species is *C. bifidus* Brongniart, 1800. The remaining Malagasy species are classified under the oldest available generic name *Calumma* Gray, 1865 with the type species *C. cucullatus* Gray, 1831. The monophyly of this last genus is, however, to be demonstrated in future studies as it is not defined by apomorph characters.

A similar problem is found in the African group of the Chamaeleoninae. One of the rami of the phylogeny (Bafr. of Fig. 19) is defined by symplesiomorphies, but we, nevertheless, treat this group provisionally as a genus. The oldest available generic name is *Bradypodion* Fitzinger, 1843, the type species being *C. pumilus* Gmelin, 1789. We must point out that *Bradypodion* as used here comprises more species than *Bradypodion* as used by, for instance, Raw (1976). For a systematic list of species see below.

The remaining African species are characterized by various configurations of large longitudinal lung septa that we consider a shared derived condition. The appropriate name for this group, which we consider a genus, is due to the inclusions of *C. chamaeleon* (Linnaeus, 1758), *Chamaeleo* Laurenti, 1768. Within the genus *Chamaeleo* (sensu novo) several subgroups can be distinguished. One is *Chamaeleo* s. str. considered here to represent a subgenus and being defined by synapomorphies such as the multi-rotulae configuration, the peculiar lung septation and the 12M + 12m karyotype. The plesiomorph four rotulae condition is retained in *C. arabicus* and *C. namaquensis*, but it does not exclude them from the subgenus as *C. namaquensis* possesses the other

two characteristics of this group, whereas *C. arabicus* is very likely to possess them as well.

The four rotulae condition is also retained in the remaining African species, which are considered a sister-group of *Chamaeleo* s. str. They are characterized by large septa connected with the ventral wall of the lung and the affinity of the three subgroups is reflected by the annulated horns found in members of all subgroups. The oldest subgeneric name for this group is *Trioceros* Swainson, 1839, the type species is *C. oweni* Gray, 1831. Within this subgenus *C. melleri* stands relatively isolated because of its unique lung septation and has a sister-group status in relation to the species-groups of *C. bitaeniatus* c. s. and *C. cristatus* c. s. Although within these last two subgroups a further differentiation can be made with the help of hemipeneal characters (papillary fields, relative size of the sulcal rotulae etc.) and lung septation characters (two large septa or one large and one small ventral septum) we shall not incorporate these infra-subgeneric subdivisions in the formal nomenclature. The same applies to the infra-generic differentiation that can be made with the help of hemipeneal papillary structures within *Furcifer* and *Calumma*.

Summarizing the above consideration results in the following classification:

Family CHAMAELEONIDAE

Subfamily Brookesiinae

Genus *Brookesia*

Species included: *antoetrae*, *betschi*, *bonsi*, *decaryi*, *dentata*, *ebenau*, *griveaudi*, *karchei*, *lambertoni*, *legendrei*, *minima*, *nasus*, *peyrierasi*, *ramanantsoai*, *stumpffi*, *superciliaris*, *therezieni*, *thieli*, *tuberculata*, *vadoni*.

Genus *Rhampholeon*

Species included: *brachyurus*, *brevicaudatus*, *kerstenii*, *marshalli*, *nchisiensis*, *platyceps*, *spectrum temporalis*.

Subfamily Chamaeleoninae

Genus *Calumma*

Species included: *boettgeri*, *brevicornis*, *capuroni*, *cucullata*, *fallax*, *furcifer*, *gallus*, *gastrotaenia*, *globifer*, *guibei*, *linota*, *malthae*, *nasuta*, *oshaughnessyi*, *parsonii*, *peyrierasi*, *tsaratananensis*, *tigris*.

Genus *Furcifer*

Species included: *angeli*, *antimena*, *balteatus*, *belalandaensis*, *bifidus*, *campani*, *cephalolepis*, *labordi*, *lateralis*, *minor*, *monoceras*,

oustaleti, pardalis, petteri, polleni, rhinoceratus, tuzetae, verrucosus, willsii.

Genus *Bradypodion*

Species included: *adolffriderici, caffer, carpenteri, damaranum, dracomontanum, fischeri, gutturale, karroicum, melanocephalum, mlanjense, nemorale, occidentale, pumilum, setaroi, spinosum, taeniobronchum, tenue, thamnobates, uthmoelleri, ventrale, xenorhinum.*

Genus *Chamaeleo*

Subgenus *Chamaeleo*

Species included: *africanus, arabicus, anchietae, calcaricarens, calyptratus, chamaeleon, dilepis, gracilis, laevigatus, monachus, namaquensis, quilensis, senegalensis, zeylanicus.*

Subgenus *Trioceros*

Species included: *affinis, bitaeniatus, camerunensis, chapini, cristatus, deremensis, eisentrauti, ellioti, feae, fuelleborni, goetzei, hoehnelii, incornutus, jacksonii, johnstoni, kinetensis, laterispinis, melleri, montium, oweni, pfefferi, quadricornis, rudis, schoutedeni, schubotzi, tempeli, wernerii, wiedersheimi.*

ZUSAMMENFASSUNG

In der vorliegenden Arbeit wird die Hemipenismorphologie von 28 *Chamaeleo*- und 2 *Brookesia*-Arten beschrieben. Hemipenismorphologische Angaben über 44 *Chamaeleo*- und 15 *Brookesia*-Arten aus der Literatur werden einbezogen. Diese Daten, die gemeinsam ca. 70 % der bekannten Chamäleonarten umfassen, werden analysiert und diskutiert, d. h., Homologien der Hemipenismerkmale werden aufgezeigt und ihre relative Apo- oder Plesiomorphie abgesichert. Sodann wird eine Phylogenie der Chamäleons auf der Basis von Hemipenismerkmalen formuliert. Dieses Phylogeneschema wird mit ähnlichen Modellen aufgrund karyologischer, osteologischer und lungenmorphologischer Merkmalsgruppen verglichen und in Deckung gebracht. Die hieraus resultierende Phylogenie der Chamäleons wird in zoogeographischer Hinsicht diskutiert, unter besonderer Berücksichtigung der Vikarianz der madagassischen und der afrikanischen Arten. Die gegenwärtige Klassifikation der Chamäleonarten in nur 2 Gattungen, nämlich *Brookesia* Gray 1864 und *Chamaeleo* Laurenti 1768 spiegelt nicht die diskutierten stammesgeschichtlichen Beziehungen wider, daher wird folgende revidierte Klassifikation vorgeschlagen: Innerhalb der Familie Chamaeleonidae werden 2 Unterfamilien anerkannt, und zwar die Brookesiinae und die Chamaeleoninae. In-

nerhalb der *Brookesiinae* werden 2 Gattungen, nämlich *Brookesia* und *Rhampholeon*, innerhalb der *Chamaeleoninae* jedoch 4 Gattungen als valide angesehen, nämlich *Calumma*, *Furcifer*, *Bradypodion* und *Chamaeleo*.

RÉSUMÉ

Ce travail décrit la morphologie de l'hémipénis de 28 espèces de *Chamaeleo* et de deux espèces de *Brookesia* puis passe en revue les données de la littérature concernant 44 espèces de *Chamaeleo* et 15 de *Brookesia*. L'analyse et la discussion de cet ensemble, qui concerne environ 70 % des Caméléons connus, conduisent à établir l'homologie des structures de l'hémipénis ainsi que leur valeur apo-ou plésiomorphique. D'où la proposition d'une phylogénie des Caméléons basée sur les caractères hémipéniens. Celle-ci est comparée avec les séries établies sur des caractères cariologiques, ostéologiques et de morphologie pulmonaire, ce qui permet de mettre en évidence l'accord des tendances évolutives. Ces différentes données sont associées pour proposer une phylogénie des Caméléons. Celle-ci est discutée à la lumière des hypothèses zoogéographiques, en particulier celle concernant la vicariance entre les espèces malgaches et africaines. La classification usuelle des Caméléons, qui les sépare en deux genres: *Brookesia* Gray, 1864 et *Chamaeleo* Laurenti, 1768, ne s'accorde pas avec les relations phylogéniques étudiées. Il en résulte une révision de la systématique de la famille des Chamaeleonidae divisée en deux sous-familles celle des *Brookesiinae* avec deux genres *Brookesia* et *Rhampholeon* et celle des *Chamaeleoninae* avec quatre genres: *Calumma*, *Furcifer*, *Bradypodion* et *Chamaeleo*.

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